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Silvics of North America

Volume 2. Hardwoods

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Silvics of North America

Volume 2, Hardwoods

Russell M. Burns and Barbara H. Honkala
Technical Coordinators
Timber Management Research

Agriculture Handbook 654

(Supersedes Agriculture Handbook 271,
Silvics of Forest Trees of the United States, 1965)

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The silvical characteristics of about 200 forest tree species and varieties are described. Most are native to the 50 United States and Puerto Rico, but a few are introduced and naturalized. Information on habitat, life history, and genetics is given for 15 genera, 63 species, and 20 varieties of conifers and for 58 genera, 128 species, and 6 varieties of hardwoods. These represent most of the commercially important trees of the United States and Canada and some of those from Mexico and the Caribbean Islands, making this a reference for virtually all of North America. A special feature of this edition is the inclusion of 19 tropical and subtropical species. These additions are native and introduced trees of the southern border of the United States from Florida to Texas and California, and also from Hawaii and Puerto Rico.

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Foreword

"Silvics of Forest Trees of the United States," Agriculture Handbook 271, was the first comprehensive document of its kind in the United States. It was an edited compendium of research papers describing silvical characteristics of 127 trees; the papers had been independently prepared by specialists at U.S. Department of Agriculture Forest Service experiment stations. The original "silvics manual" took 10 years to complete and was published in 1965.

Our store of silvical and related knowledge has markedly increased since that silvics manual was published 25 years ago. The "Woody-Plant Seed Manual" of 1948 was updated in 1974 and issued as Agriculture Handbook 450, "Seeds of Woody Plants in the United States." New names were added to the literature in 1979 with Agriculture Handbook 541, "Checklist of United States Trees (Native and Naturalized)," which superseded Agriculture Handbook 41. In 1980, the 1954 Society of American Foresters' publication, "Forest Cover Types of the United States and Canada," was revised. A six-volume "Atlas of United States Trees" (U.S. Department of Agriculture Miscellaneous Publications 1146, 1293, 1314, 1342, 1361, and 1410) added tree range maps of most major and minor tree species to the literature. It was both appropriate and timely, therefore, to revise the information in the original silvics manual and to add other native and naturalized trees to the compendium.

"Silvics of North America" describes the silvical characteristics of about 200 conifers and hardwood trees in the conterminous United States, Alaska, Hawaii, and Puerto Rico. Individual articles were researched and written by knowledgeable Forest Service, university, and cooperating scientists. They were reviewed by their counterparts in research and academia. The project took 10 years to complete. The revised manual retains all of the essential material from the original publication, plus new information accumulated over the past quarter of a century. It promises to serve as a useful reference and teaching tool for researchers, educators, and practicing foresters both within the United States and abroad.

Jerry A. Sesco
Deputy Chief for Research

The use of trade names in this publication is for the information and convenience of the reader, and does not constitute official endorsement or approval by the U.S. Department of Agriculture of any product to the exclusion of others that may be suitable.

This publication also reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

Acknowledgments

This handbook is the result of a servicewide project of Timber Management Research, Forest Service, U.S. Department of Agriculture. It is an expansion of "Silvics of Forest Trees of the United States," originally published in 1965, and supersedes that handbook.

Individual papers contained in the two volumes of "Silvics of North America" were written by research foresters at U.S. Department of Agriculture Forest Service experiment stations and at several universities. Technical content was edited by Russell M. Burns, Silviculturist, and compilation and coordination of the project were by Russell M. Burns and Barbara H. Honkala, Botanist, of Timber Management Research, Washington, DC. Barbara Honkala revised the tree range maps and prepared lists of botanical, bird, and mammal names. Burns and Honkala prepared the glossary and the summary of shade tolerance classes, tree and flowering characteristics, type of seed germination, and order of soils on which trees most commonly grow. Robert L. Lyon, Entomologist, Arthur L. Schipper, and Charles S. Hodges, Jr., Pathologists, Forest Insect and Disease Research, Washington, DC, and Harold H. Burdsall, Jr., Mycologist, Process and Protection Research, Forest Products Laboratory, Madison, WI, reviewed and listed names of insects, mites, and organisms causing tree diseases. William G. Hauser, formerly of the Forest Service Permanent Image Collection, Washington, DC, assisted with the acquisition of photographs. Elbert L. Little, Jr., Dendrologist (retired), assisted in proofreading.

During the last year and a half, the project was directed by Robert D. Wray, Leader, Information Services (retired), North Central Forest Experiment Station. Wray edited the final revisions and guided the book through the production and printing processes. The North Central Station also provided clerical and administrative support during the pre-publication process. Robert P. Schultz, Assistant Director for Research, Southern Forest Experiment Station, served as technical reviewer and advisor for the final revisions.

The entire final proof was proofread under the direction of Mary Peterson and Barbara Winters, assisted by Gayla Conners, Rose Berg, Patricia Halter, Phyllis Moline, and Rita Ronning—all of the North Central Forest Experiment Station. Personnel from the various Forest Service Experiment Stations carefully monitored the final revision and review of the chapters emanating from their Stations. Notable among these were: Margaret Buchanan, Northeastern Station; Louise Foley, Southeastern Station; Carlow Lowe and Jody Jones, Southern Station; Robert Hamre and Wayne Shepperd, Rocky Mountain Station; Richard Klade, Intermountain Station; Martha Brookes, Pacific Northwest Station; and Sandra Young, Pacific Southwest Station.

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The Tree and Its Environment

H. A. Fowells and Joseph E. Means

The mature forest tree is an outstanding example of interaction between the hereditary characteristics of an organism and its environment. The tiny embryo of the seed of the giant sequoia (*Sequoiadendron giganteum*) contains the potential to develop into the most majestic of plants. But if the environment is unfavorable, this potential will not be realized. Thus, responses of different species to environmental influences determine in part the success of silviculture. Silviculturists must know how the environment will affect the growth and development of trees they wish to manage.

Effects of environmental factors are generally the same for all trees. Reports in this publication describe known responses of each species to specific environmental conditions. This introduction provides background information of a general nature. The information offered here cannot approach the scope of texts on forest tree physiology, such as those by Kramer and Kozlowski and by Thimann (see General Notes and Selected References). Recently, Kozlowski (*26*) outlined specific effects of some environmental stresses on tree growth and development. More information on forest ecology is available in texts by Daubenmire and by Spurr.

The Total Environment

The total environment of a tree is a complex integration of physical and biological elements. The physical elements are related to climate and soil and include radiation, precipitation, and the movement and composition of air, as well as the texture of the soil and its structure, depth, moisture capacity, drainage, nutrient content, and topographic position. Biological elements are the plant associates; the larger animals that use the forest as a source of food and shelter; the many small animals, insects, and insectlike animals; the fungi to which the trees are hosts; and the microorganisms in the soil.

Complete and exact quantification of the environment is practically impossible. Some combinations of specific conditions have been used to characterize broad environmental regions and have been related to forest cover or vegetation type. Temperature indices were the basis for one classification system in which the climate of the United States was divided into seven temperature zones, each with its characteristic forest species, minor vegetation, and animal life (*39*). In another system the North American continent was divided into six zones on the basis of the average temperatures of May, June, July, and August (*38*). In a more complex scheme, winter temperatures, summer and winter dryness, and relative summer temperatures were considered (*24*). Under this classification the southeastern United States is a single zone characterized by moderate or cool winters and moist warm summers.

A more widely used classification system is based upon precipitation effectiveness (P–E), a function of precipitation and evaporation, which represents the amount of precipitation available to plant growth (*69*). Five climatic regions are recognized: superhumid, humid, subhumid, semiarid, and arid. These are associated with corresponding vegetation types: rain forest, forest, grassland, steppe, and desert. The subhumid region, or grassland, is divided into a moist subhumid and a dry subhumid. Some ecologists believe the moist subhumid region to be a forest region from which forests have been excluded by causes other than climate.

The superhumid region in North America includes the coastal forests of southern Alaska, Canada, Washington, Oregon, and northern California; the western slope of the Cascade Range in Oregon and Washington and of the Sierra Nevada in California; and also isolated areas in the Rocky Mountains, Appalachian Mountains, and New England. Western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), coast redwood (*Sequoia sempervirens*), western redcedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) are principal tree species in the western coastal part of the region. Western white pine (*Pinus monticola*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and white fir (*Abies concolor*) are included with other species in mountain portions of the western part of the region. In the east, Fraser fir (*Abies fraseri*), balsam fir (*A. balsamea*), and red spruce (*Picea rubens*) are found in the superhumid region.

The humid region in the East includes most of the forest land, aside from the small areas of the super-

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The authors are H. A. Fowells, Chief, Branch of Silviculture, Timber Management Research (retired), USDA Forest Service, and Joseph E. Means, Research Forester, Pacific Northwest Research Station, Portland, OR. Fowells compiled the 1965 "Silvics of Forest Trees of the United States" and rewrote and updated the introduction for this revision. Means wrote the new section on "Potential Effects of Climate Change."

humid region described above. The humid region has been subdivided into four zones, with the oak–hickory type in the area with the lowest P–E index and the spruce–fir type in the area with the highest. In the West the broken topography of mountain ranges results in many discontinuities in the humid region. Here ponderosa pine, western larch *(Larix occidentalis)*, Douglas-fir, incense-cedar *(Libocedrus decurrens)*, and lodgepole pine *(Pinus contorta)* are typical species.

Within these broad provinces or regions, the interplay of local factors and general conditions often determines whether a species will be successful on a specific site. Thus, south-facing slopes tend to be warmer and drier than north-facing slopes, and low spots or openings in the forest may be frost pockets that restrict establishment of certain species. Soil drainage or depth is often decisive in limiting the presence or growth of trees in areas where climatic conditions are of near-critical importance.

Individual Environmental Factors

The impact of a change in environment can seldom be related directly to a single measurable factor in the total complex. Subtle interrelationships between environmental factors are usually present. Knowledge of how a plant responds generally to various individual factors is useful, however.

Temperature

Temperature directly affects the day-to-day physiological processes of plants and indirectly influences their seasonal or cyclic development. Plant processes, to the extent to which they are chemical reactions, tend to follow the van't Hoff law, namely, that the rate of reaction doubles for each temperature increase of 10° C (18° F). In such reactions the temperature coefficient is two.

In biological systems the law often operates only within narrow ranges, determined by the ability of the organism to survive. Thus, the temperature coefficient of respiration is two or more up to a temperature at which some essential respiratory enzyme is denatured. The process of photosynthesis has a temperature coefficient of less than two. Growth of cells has a temperature coefficient of about two, and even the overall growth of plants may show this response within the moderate temperature range. Because the temperature coefficient for photosynthesis is less than that for respiration, high temperatures may result in less photosynthate for growth.

For each plant there is a set of cardinal temperatures that controls its growth and development and, in fact, its existence: the minimum and maximum temperatures limiting growth and the optimum temperature for growth. For alpine plants the minimum temperature is close to 0° C (32° F), the maximum 20° to 30° C (68° to 86° F), and the optimum 10° C (50° F). For temperate plants the minimum temperature is about 4° C (40° F), the maximum 41° C (106° F), and the optimum 25° to 30° C (77° to 86° F). For tropical plants the minimum is 10° C (50° F), the maximum 50° C (122° F), and the optimum 30° to 35° C (86° to 95° F).

In a dormant or resting state, plants can endure extremes much greater than the minimum and maximum temperatures for growth. Evergreen trees endure winter temperatures of –51° to –57° C (–60° to –70° F), but temperatures of –4° to –1° C (25° to 30° F) kill twigs during the growing season. During summer in the temperate zones, temperatures may exceed 46° C (115° F), but growth is often completed before maximum temperatures occur.

Resistance to freezing temperatures, or frost hardiness, may result from a change in the protoplasm. The osmotic concentration of the cell sap increases with the hydrolysis of insoluble carbohydrates to soluble sugars *(13)*. Dehydration of the protoplasm leads to an increase in the apparent bound water content of the proteins. Frost injury results from the formation of ice crystals within the protoplasm or the dehydration of the cell by ice formation in the intracellular spaces *(34)*.

Heat resistance also appears related to a change in cellular proteins. The killing of cells by heat is brought about by denaturation of the proteins.

Thermoperiodicity

Plants not only respond to maximum, minimum, and optimum temperatures, but some also grow or develop best with an alternation of daily or seasonal temperatures. The growth of tomatoes was greatest when day temperatures were 27° C (80° F) and night temperatures were 17° to 20° C (63° to 68° F) *(73)*. Similarly, loblolly pine *(Pinus taeda)* seedlings grew most with a day temperature of 27° C (80° F) and a night temperature of 17° C (63° F) *(27)*. Several explanations have been offered for this phenomenon. The difference between the temperature coefficient of photosynthesis and that of respiration provides one explanation. Although photosynthesis increases with temperature, the rate of increase is not as great as that for respiration. Moreover, respiration continues 24 hours a day. When high day temperatures are followed by low night temperatures, therefore, more photosynthate remains for growth than when both day and night temperatures are high. Another explanation stems from an apparent decrease in translocation with increased temperature. Lower night temperatures would permit more rapid translocation of photosynthates from the leaves to meristematic tissue, favoring greater growth.

Some trees and shrubs fail to develop properly if they are not exposed to low temperatures during their dormant period. Thus, some deciduous fruit trees will not break dormancy if they are not subjected to near freezing temperatures for a minimum number of hours. Observations unsupported by controlled experiments suggest that some northern or subalpine conifers require a cold treatment to break dormancy and induce seasonal growth. It also has been demonstrated that certain nondeciduous shrubs, like camellia, show optimum blooming with cyclic temperatures *(7)*. Flower buds of camellia are initiated at temperatures of 24° to 27° C (75° to 80° F), but blooming is optimum at temperatures of 10° to 16° C (50° to 60° F).

Light

Visible light, that part of the electromagnetic spectrum with wavelengths in the range of about 400 to 760 millimicrons, plus ultraviolet and infrared light, affect the growth of trees in several distinct ways. The role of light as the source of energy for growth in photosynthesis is commonly known, but its role in regulating growth is more subtle.

Quality, intensity, and duration of light energy bear upon the photosynthetic process. Chlorophyll absorbs light more readily at wavelengths between 420 and 480 millimicrons and between 620 and 700 millimicrons. Light energy of these parts of the spectrum, corresponding to the blue-violet and the orange-red, is most efficient in the photosynthetic process. There is evidence that the color of foliage of various conifers and broadleaf trees results in differential responses to parts of the spectrum *(10)*.

Understory trees are probably exposed to light of quite different quality than overstory trees. Crowns of the overstory absorb part of the blue and red light and reflect or transmit green and yellow. Thus, light in the understory is relatively higher in green and yellow light.

Intensity of the light, or irradiance, measured in terms of energy per unit area per unit time, as gram-calories per square centimeter per minute, also affects the rate of photosynthesis. The irradiance on a clear summer day at sea level in the middle latitudes is about 1.5 g-cal per cm^2 per minute. This corresponds to an illumination value of about 10,000 foot-candles as commonly measured with a light meter.

Trees vary with respect to the light intensity at which maximum photosynthesis occurs. The rate of photosynthesis of loblolly pine increases with increasing light intensity up to full sunlight. The rate of photosynthesis of associated hardwoods, such as oaks *(Quercus)* and dogwood *(Cornus)*, however, does not increase at light intensities higher than about 30 percent of full sunlight *(28)*. Similarly, Engelmann spruce *(Picea engelmannii)* reaches near maximum photosynthesis at 4,000 to 5,000 foot-candles but lodgepole pine does not appear to be light saturated at 12,000 foot-candles *(55)*. For Japanese larch *(Larix leptolepis)*, the saturation point of light intensity is twice as high as that for white fir, Sitka spruce, or western hemlock. There is evidence that the metabolic pathway in larch may be different from that of nondeciduous conifers *(14)*.

Differences in photosynthesis among tree species are related to the arrangement of the leaves and resultant mutual shading; to the morphology of the leaves, as sun-leaves and shade-leaves; and perhaps to the chlorophyll concentration of leaves. One of the characteristics of trees termed "shade tolerant" is undoubtedly their ability to carry on photosynthesis at low levels of illumination. Seedlings of red alder *(Alnus rubra)*, a shade-intolerant tree, attain a higher rate of photosynthesis per unit of foliage weight than do seedlings of Douglas-fir, Sitka spruce, or western hemlock. Rates are similar per unit of foliage area, however. Also, the photosynthetic rate of red alder is much higher at light intensities greater than 5,100 foot-candles *(30)*.

The ability of tolerant trees to grow rapidly under low light intensities may be enhanced by the greater carbon dioxide concentration under a forest canopy. There is evidence that photosynthesis increases if the carbon dioxide concentration is more than the normal 330 parts per million found at sea level. Very high light intensities may in fact inhibit photosynthesis. Seedlings that normally develop under an overstory may not photosynthesize at a maximum rate if exposed to the full-light conditions of clearings or openings *(25)*.

There is conflicting evidence concerning efficiency in photosynthesis among provenances of various species. Genetic variation in photosynthetic efficiency was found in families of Douglas-fir seedlings; however, selection for that efficiency will be valuable only if seedling values are strongly correlated with mature growth *(9)*. Photosynthetic rates of Douglas-fir from western Oregon were higher than those from western Montana. Environmental conditions affected photosynthetic rates more than the seed source *(66)*. For jack pine *(Pinus banksiana)*, the rates of photosynthesis varied among provenances according to the time of year *(35)*. Differences in rates also were observed in Scotch pine *(Pinus sylvestris)* from Poland and from Turkey *(2)*. In Douglas-fir, rapid growth appeared to be related more to photosynthetic area than to efficiency of the foliage *(18)*.

The duration of illumination also affects the total amount of photosynthesis. Plants carry on photosynthesis continuously when exposed to light for 24 hours a day. However, the effect of the duration of illumination on photosynthesis and its resultant effect on growth probably is confounded with the temperature-regulating effect of day length on growth.

Light regulates growth and development of a tree through a number of incompletely understood reactions. One of these is the photoperiodic control of growth and flowering. Many tree species either cease terminal growth or continue to grow, depending on the duration of light within a day. A number of angiosperms and gymnosperms cease growth when exposed to only 8 hours of light a day *(11)*. Scotch pine, loblolly pine, and Virginia pine *(Pinus virginiana)* seedlings grow continuously on 14-hour days and with repeated flushes on 16-hour days. Some broadleaved trees, such as red maple *(Acer rubrum)*, birch *(Betula)*, elm *(Ulmus)*, and catalpa *(Catalpa)*, grow continuously with exposure to 16-hour days, while others, such as sweetgum *(Liquidambar styraciflua)* and horsechestnut *(Aesculus hippocastanum)*, do not.

Thus, the photoperiodic control of terminal growth of trees may be a limiting factor in the north-south movement of a species, even within its natural range. For example, under natural day length, loblolly pine from Maryland grew poorly in northern Florida compared to local loblolly pine, but it quadrupled its growth when the natural day length was extended with artificial light *(50)*. Similarly, cuttings of black cottonwood *(Populus trichocarpa)* from coastal Alaska, latitude 60° 37′ N., stopped growth about June 20 when planted near Boston (lat. 42° N.) but continued growing for 2 months more when day length was increased to match that of the source of the cuttings in Alaska *(49)*. Day length also influenced the time of bud set in western hemlock, which has a long north-south range. Because bud set precedes the onset of dormancy and cold hardiness, this species should not be moved far in a north-south direction *(31)*. Variation in height growth resulting from day length may limit the selection of provenances of white spruce *(Picea glauca)* *(53)*.

Day length, or photoperiod, also influences growth in diameter. Under long-day conditions trees produce large-diameter, thin-walled cells, resembling springwood. A change to short-day conditions results in the formation of small-diameter, thick-walled cells resembling summerwood. The transition is related to the production of growth-regulators during the period of terminal elongation *(32)*.

The transition from large-diameter cells to small-diameter cells with changing day length has been noted in a number of species, including red pine *(Pinus resinosa)* *(32)*, Monterey pine *(P. radiata)* *(19)*, Caribbean pine *(P. caribaea)* *(3)*, and European larch *(Larix decidua)* *(77)*. The content of inhibitors seems to be related to the production of thick-walled cells, whereas the content of promoters appears related to shoot growth. The amount of growth substances has been shown to be related to photoperiod *(77)*. One might speculate that the absence of definite growth rings in many tropical trees is related to a more or less constant day length.

Little evidence is available to show photoperiodic control of flowering in forest trees. Judging from the widespread occurrence of the phenomenon of photoperiodism in many plants, it is probable that such control does exist. However, flowers were borne on trees of 34 species of pine growing in California at a latitude of about 38° N., even though the trees represented pine sources ranging from latitude 15° N. to 70° N., with corresponding differences in day length *(42)*.

Unequal distribution of light may indirectly affect the form of trees. Greater development of the crown on the lighted side of the tree than on the shaded side results in asymmetrical growth of the bole. Regular spacing of trees to ensure better distribution of light thus tends to promote good form.

Light may also be a factor in epicormic sprouting. On many tree species, dormant buds on the bole are stimulated and sprouts develop after trees are exposed when surrounding trees are cut.

Moisture

Although the presence of one component of the environment is no more essential than that of another to the growth of trees, moisture is very often a limiting factor. Within the continental United States, excluding Alaska, annual precipitation to which forests are exposed varies from an average maximum of about 3550 mm (140 in) to an average minimum of about 380 mm (15 in). Rather large areas of forests, particularly ponderosa pine, grow with less than 500 mm (20 in) of annual precipitation. Silvicultural measures that make more of the total moisture available to the tree crop very likely increase growth.

Total precipitation is often used as a measure to relate productivity of forests to moisture, but it is not completely satisfactory. Moisture is available to trees primarily through the soil, although there is some evidence that they absorb atmospheric moisture under conditions of moisture stress *(65)*. The moisture-holding properties of the soil mantle are therefore of major importance.

Seasonal distribution of precipitation has a bearing upon the effectiveness of total precipitation. In forests of the Sierra Nevada in California, summer rains are rare. Nearly all the moisture available for trees is the amount held in the soil from winter and spring precipitation. In some parts of the country the highest precipitation occurs in the summer months. In much of the East, on the other hand, precipitation is rather evenly distributed throughout the year. The growth of loblolly, slash, shortleaf, and longleaf pines *(Pinus taeda, P. elliottii, P. echinata,* and *P. palustris)* has been shown to be differentially related to the amount and seasonal distribution of rainfall as well as to its retention in the soil *(59)*.

In addition to precipitation ordinarily measured as rain or snow, forests in some sections of the country obtain moisture from "fog-drip." Along the Pacific coast, the redwood forests in California and the Sitka spruce–hemlock–Douglas-fir forests of Oregon, Washington, and British Columbia undoubtedly benefit from the water condensed from fog dripping to the ground. However, fog-drip is only a part of the climatic environment of these fast-growing forests. The longer growing season, mild summer and winter temperatures, heavy precipitation, and high relative humidity (which lowers evapotranspiration rates), in addition to the fog-drip itself, certainly favor the exceptionally high forest productivity of this narrow belt along the coast.

Water available to trees is either that held temporarily in the soil mass against the force of gravity or that held between the soil particles by surface tension (capillary water). Gravitational water drains out of the soil mass following a rain. Capillary water is generally available except after rains or periods of melting snow. Water held at two other levels of energy, hygroscopic water and water of hydration in certain minerals, is not available to trees.

Water generally available to trees is held by energy forces that range from 1.1 to 15 atmospheres. The lower level approximates the field capacity of the soil, or the amount of water held against gravity. The upper level approximates the permanent wilting point, or the soil moisture level at which a plant is no longer able to obtain water fast enough to prevent wilting, from which it cannot recover unless water is added. Theoretically, plants cannot recover even when water is added if the permanent wilting point is exceeded.

The permanent wilting point is not well defined, however, for plants that have thickened rigid leaves, such as those of conifers and evergreen broadleaf trees and shrubs. There is evidence that such plants can live in a quiescent state and can extract water from the soil beyond the permanent wilting point as determined conventionally *(61)*. This enables the tree to survive temporary droughts that might cause the death of more succulent plants.

Water serves as a solvent for minerals, gases, and various organic compounds; it is a major part of the protoplasm of cells and is essential to certain metabolic processes. Most of the water taken up by a tree is transpired, however, and the benefit to a tree of such water use is not fully understood. In pine and hardwood forests in Arkansas, for example, 4.8 mm (0.19 in) of moisture was used per day from the upper 1.2 m (4 ft) of soil during the early part of summer *(79)*. The loss from the 1.8-m (6-ft) soil layer was estimated to be 6.4 mm (0.25 in) per day, or about 63 500 liters of water per hectare (6,800 gal/acre) per day.

The transpirational use of water may be of no immediately apparent benefit to a tree, but the conditions leading to transpiration are conducive to growth. The rate of photosynthesis is greater during periods of low moisture stress than when moisture stress forces the closing of the stomata. Transpiration thus may appear to be a necessary accompaniment to the availability of moisture for growth processes and the conditions promoting gas exchange and photosynthesis. There is evidence that moisture stress late in the growing season increases the cold hardiness of seedlings *(6)*.

Soil Condition

In addition to being a reservoir for moisture for trees, soil provides all the essential elements required in growth except those from the atmosphere, carbon from carbon dioxide, and some oxygen. Obviously, soil also provides the medium in which a tree is anchored. The many characteristics of soil, such as chemical composition, texture, structure, depth, and position, affect the growth of a tree to the extent to which they affect the supply of moisture and nutrients. A number of studies have shown strong correlations between productivity of site or growth of trees and various soil characteristics such as depth and position on the slope. The relationships are often indirect.

Generally, soil contains all the chemical elements essential to the growth of plants. Some elements may not be present in large enough quantity to sustain growth, however. For example, zinc, which is necessary in only minute amounts, was so deficient in western Australia that the growth of pines was inhibited *(64)*. In the United States, deficiencies of potassium, phosphorus, and nitrogen have been observed, and the application of fertilizers has resulted in increased growth, greater fruit production, and more desirable foliage color *(74)*. The effects of fertilization may continue for some time; increased growth of black spruce *(Picea mariana)* continued for 9 years after fertilization with major elements *(72)*.

The level of soil nutrients sufficient for optimum growth of most species is not known. Some guides to the adequacy of nutrient levels may be obtained from foliar analysis. Admittedly the technique has flaws, but a number of studies in the forest and in pot culture show that the optimum growth of pine occurs when adequate nutrient availability is reflected by the following foliar concentrations: nitrogen, 2 to 2.5 percent; phosphorus, 0.13 to 0.2 percent; potassium, 1 percent; calcium, 0.3 percent. In white and red spruce the transition zone from deficiency to sufficiency seems to begin at these foliar concentrations: for nitrogen, 1.3 percent; for phosphorus, 0.14 percent; for potassium, 0.30 percent; for magnesium, 0.06 percent; and for calcium, 0.10 percent *(68)*. Foliar concentrations of potassium and phosphorus were found to be correlated with growth characteristics of white fir, but no close relation was shown with most soil elements *(22)*.

In some soils the concentration of certain elements may be too high to support vigorous growth of trees. Soils derived from serpentine often contain so much magnesium that growth is poor, perhaps because the competition of the magnesium depresses calcium intake resulting in calcium deficiency.

The ability of a soil to supply water and nutrients is strongly related to its texture and structure as well as to its depth. Coarse-textured soils, the sands, are low in nutrient content and in water-holding capacity. Fine-textured soils, the clays, may be high in nutrient content and have high water-holding capacity. Aeration is impeded in heavy clays, particularly under wet conditions, so that metabolic processes requiring oxygen in the roots are inhibited.

In clay soils, percolation of water into the soil, and soil aeration, are favored by aggregated soil particles rather than by a plastic structure or cemented layers of hardpans. Silvicultural practices to prevent the destruction of organic matter and the compaction of soil can provide better conditions of soil moisture and aeration.

Air Movement

The movement of air is usually not an important environmental factor except under extreme conditions. It has a minor effect in that an increase in wind velocity results in greater evaporation and transpiration, taking water that might otherwise be used for growth. Prevailing winds from a given direction usually result in deformation of the crown of a tree and uneven development of its bole. Although the direct physical effects of wind in uprooting or breaking trees may be calamitous, adjustment of silvicultural practices to avoid such damage is not feasible. Where prevailing winds are known to be strong, however, windfirm trees can be favored and cutting patterns adjusted to minimize effects *(15)*.

Potential Effects of Climate Change

Climate (temperature, precipitation, and wind), and atmospheric chemistry (including carbon dioxide (CO_2) supply and air pollution) directly affect plant life. They also indirectly affect plants through their impact on soils and soil biota, pests and other pathogens, and other disturbances. Important changes in the Earth's climate due to increases in "greenhouse" gases are inevitable, according to most climatologists *(17,43,57,62)*. Simulation models suggest that the climate of the Earth is beginning to change at a rate unprecedented in the history of contemporary plant and animal species *(51,57)*. These changes would significantly affect reproduction, growth, and mortality of forest trees *(76)*. Thus, many of the data and relations described in this manual will be altered if climate and atmospheric chemistry change as projected.

How May Climate Change?

Mean annual global temperature is projected to rise 2° to 6° C (4° to 11° F) by the middle or end of the 21st century *(17,43,57,62)*. Most models predict the warming will be greater at higher latitudes, but there is less agreement on changes in the spatial and seasonal patterns of temperature and precipitation for areas the size of the United States *(57)*. Given the rapid rate of projected changes, plant adaptations in physiology and range will have to be made within one or two lifetimes of most tree species. This contrasts sharply with changes following the last ice age when similar temperature increases occurred over 7000 years, giving forests and trees many generations to adapt. Further, climate change will probably continue as people add more of the greenhouse gases to the atmosphere.

Natural Range

Species ranges are likely to be modified greatly if projected climate changes occur. Zabinski and Davis *(78)* projected drastic reductions in the natural ranges of eastern hemlock *(Tsuga canadensis)*, American beech *(Fagus grandifolia)*, yellow birch *(Betula alleghaniensis)*, and sugar maple *(Acer saccharum)* if CO_2 doubled as two different atmospheric general circulation models predicted. The reductions in present range varied from 20 to 70 percent, with similar expansions of potential natural range as range boundaries shifted northward hundreds of kilometers. For the western United States under a doubled-CO_2 climate, Leverenz and Lev *(33)* projected significant changes in range or importance of Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, ponderosa pine *(Pinus ponderosa)*, western larch *(Larix laricina)*, and Engelmann spruce *(Picea engelmannii)*.

Although the natural ranges of many species will likely shift northward and upslope, some populations may not be able to expand into newly suitable areas because of the limited speed of natural migration compared to the speed of climate change *(78)* and barriers to migration, such as lowlands with inhospitable climate and agricultural and urban areas *(51,52)*.

Though mature trees may survive for long periods *(8)*, a population must be able to complete its life cycle in the new environment to survive. Populations at risk of local extinction include those near mountain tops where suitable climate may move above the mountain tops or zones of suitable soil, and those in isolated reserves. Populations that will be at low risk include those able to reproduce in the changing climate at their current sites, those far enough down mountain slopes that suitable habitat will occur upslope within dispersal distances as climate warms, those able to disperse over large distances, and those assisted by people.

Soils

Another component of environmental change, atmospheric pollution, will continue to affect trees, in part through its effect on soils. Acid deposition, including nitrate and sulfate, may acidify soils and leach nutrient cations, thus decreasing soil fertility in the long term *(5,54)*. Acidification also increases soluble aluminum that can be directly toxic to trees *(21)* and interfere with calcium uptake, reducing cambial growth, sapwood cross-sectional area, and leaf area, in turn. This latter mechanism has been suggested as a cause of red spruce decline in the northeastern United States *(58)*.

Moderate amounts of pollutant nitrogen deposition may increase available soil nitrogen *(1,5)*. In contrast, excess soil nitrogen from atmospheric pollution in the northeastern United States may have several detrimental effects on plants in addition to those already mentioned *(1)*. It may cause a decrease in fine-root biomass and energy allocated to mycorrhizal associates, leading to decreased uptake of phosphorus and water *(1)*, and it may predispose conifer foliage to winter damage *(13)*.

Soil organic matter increases markedly (up to 3-fold) from grasslands through forests on mountain slopes *(20)*. This is controlled in part by decreasing temperature. If temperature increases as projected, decomposition of litter and soil organic matter will speed up. This may cause equilibrium organic matter content to decrease in the absence of compensating increases in productivity. If this occurs, the increased nitrogen released may temporarily but significantly increase forest growth. Soil organic matter and available soil nitrogen are projected to change ± 80 percent and ± 36 percent, respectively, in some northern forests under a doubled-CO_2 climate, depending on latitude and soil water-holding capacity *(48)*.

Damaging Agents

Growth and fuel accumulations may increase in the future on sites with equivalent droughtiness because increased CO_2 fertilization often increases net photosynthesis and decreases water use *(29,67)*. Death of established trees from stresses caused by environmental change would add to these fuels. Higher fuel loadings and warmer climate would probably increase wildfire intensity. Wildfire frequency for a region may also increase as climate warms (assuming the currently widespread relation between increased drought and increased fire frequency still holds) *(36)*, and precipitation does not increase.

Pest outbreaks may increase in forests where existing drought increases *(37)*. Fertilization by CO_2, however, may partially compensate for physiological stress caused by drought and higher temperature *(29)*. Forest pests, such as the balsam woolly aphid *(44)* and pine wilt disease *(56)*, that have ranges controlled by climate will probably have range shifts. Precipitation and temperature are known to influence population of some forest pests, for example southern pine beetle *(Dendroctonus frontalis)* *(40)* and gypsy moth *(Lymantria dispar)* *(4)*, so climate changes may significantly affect magnitude and frequency of pest outbreaks.

Changes in frequencies and intensities of other natural damaging agents (high-speed winds, temperature extremes, lightning, ice storms, and droughts) may also occur with climate change and thus adversely affect forest trees *(41)*.

Continued atmospheric pollution will compound some of these effects. For example, studies have shown that pollutants can reduce the growth of ponderosa pine and increase infection and mortality from bark beetles *(16)*.

Growth and Biomass Accumulation

Simulation experiments in eastern North America suggest that doubling or quadrupling CO_2 may increase biomass of natural northern stands by 70 percent or more (50 to 80 Mg/ha (30 to 45 ton/acre)) and decrease biomass of natural southern stands by 60 percent or more, depending on specific conditions *(48, 63)*. Factors not included in these simulations, such as the potential increased ability of trees to tolerate drought under increased CO_2, may lessen growth reductions in southern stands *(11,38)*.

Increased CO_2 has also been shown to increase nitrogen fixation in black alder *(Alnus glutinosa)* and black locust *(Robinia pseudoacacia) (45)* and mycorrhizal colonization in white oak *(Quercus alba) (47)*. Moreover, carbon dioxide fertilization increases the ability of seedlings of some species to tolerate drought *(29,67)* and nutrient deficiency *(46)*.

Competition

Competition among many species may change significantly as CO_2 changes. Under high light in a greenhouse experiment with 1-year-old saplings, red oak *(Quercus rubra)* grew as fast as yellow-poplar *(Liriodendron tulipifera)* under ambient CO_2, but grew faster than yellow-poplar under doubled CO_2. Similar differences occurred with other species *(75)*. Elevated CO_2 commonly increases water-use efficiency of seedlings *(29,46,67)* but species differences are common. Water-use efficiency of water-stressed sweetgum *(Liquidambar styraciflua)* seedlings was increased more by elevated CO_2 than was that of loblolly pine *(Pinus taeda) (71)*. Thus, growth of sweetgum was reduced less by water stress than was that of loblolly pine *(70)*. This may allow sweetgum under elevated CO_2 to compete more favorably against loblolly early in succession on drier Piedmont sites. However, it is not known how these differences in seedling responses will affect competitive interactions over the lifetimes of large trees in ecosystems.

Genetics

As climate changes in some locales—for example, as temperature increases in boreal forests in Canada *(63)*—existing individuals may become better adapted and stand productivity may increase. In other areas, such as near the hot or dry limits of a species' range, existing individuals may become less well adapted *(33)* and productivity may decline *(63)*. Species with broadly adapted genetic bases, such as loblolly pine, sweetgum, and Douglas-fir, may be better able to adapt to environmental change than other forest trees *(23)*. People managing large tree-breeding programs with narrowly defined breeding zones (e.g., *60)* may find selected trees are poorly adapted to their original zones. Such programs, however, will provide an extremely large pool of measured and structured genetic diversity, potentially helpful to managers in finding trees adapted to changed climate. Determining the locales where a genotype or species will do well may be difficult, because its optimum environment will shift over the landscape if climate continues to change over a rotation. Adaptation of species to changing climate may be approached, however, by tree-breeding and silviculture programs that seek to maintain high genetic diversity within stands *(23)*, produce more heterozygous trees, and attempt to select genotypes that will be adapted to future environments.

Most of the potential responses to environmental change presented here are projections based on incomplete current knowledge, not reliable predictions. However, many projections suggest important changes in the silvical characteristics of trees and the ways we must manage them. The speed of environmental changes may cause responses, such as wildfire, that produce major change in landscapes before noncatastrophic responses cause similar alterations in established forests. Also, some of the most significant responses to environmental change will likely be surprises. So, people using this manual would do well to keep abreast of new research on expected environmental changes and impacts on trees and forests. Such information will be essential to adapt management to environmental changes, and there will be many opportunities to do so.

Conclusion

This general statement of the responses of trees to environmental factors has provided a basis for consideration of the detailed and specific information about individual species presented in the papers that follow. Knowledge of species' responses to environmental influences can guide silvicultural practices and determine their success. Thus, in efforts to favor pine in the mixed conifer forests of the west slope of the Sierra Nevada in California, it was found that white fir seedlings were very sensitive to late spring frosts, which seldom hurt ponderosa pine *(12)*. Overstory trees or understory brush can protect the firs against frost. Complete clearing, as by patch cutting, removes the protection and creates conditions in which fir regeneration cannot compete successfully with pine regeneration. In another instance, high light intensities as found in clearings inhibited Engelmann spruce but not lodgepole pine *(55)*.

Although much has been learned about environmental responses of individual species, information for some species is still extremely sketchy. Progress toward more intensive silviculture depends on our ability to fill in the gaps in our knowledge of silvics. In the words of Aristotle, the search for truth is in one way hard and in another easy. For it is evident that no one can master it fully nor miss it wholly. Each adds a little to our knowledge of nature and from all the facts assembled there arises a certain grandeur.

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General Notes and Selected References

This edition of the "silvics manual" differs from the original in length, format, and the number of species included. A wider geographical area is covered and species with other than commercial timber value have been added. To keep the present work to a reasonable length, descriptions and illustrations of genera and many of the pre–1965 citations contained in the earlier edition were omitted.

The task of preparing so extensive a collection of individual papers was formidable, and many decisions were dictated by practical considerations. Although the individual papers follow the same general pattern, no attempt was made to achieve uniformity of length, scope, or approach. Many differences in treatment are related to the importance of the species and the amount of information available in the literature. The following notes on specific points should be helpful.

Varieties

The importance of a variety within a species differs. Some varieties, particularly those important to forestry, are addressed separately. Others are discussed within the species treatment, or are described under the heading "Genetics." The term subspecies used in some instances is synonymous with variety.

Species Names

Within the text, scientific names of trees and other plants, insects, and diseases are given without specification of author or synonyms; these are provided in lists at the end of each volume. Scientific names are generally those that were in effect when the original writing was done. Common names of birds and mammals are used in the text; scientific names are provided in a list. Every effort has been made to achieve accuracy and consistency in use of scientific names, but as common names differ widely, uniformity was not attempted. References used for all names are included in the list that follows these notes. Names of trees follow "Checklist of United States Trees"; other plant names were checked against the "National List of Scientific Plant Names"; and mammal names were taken from the "Checklist of Mammals of the United States and the U.S. Territories."

Measurements

Metric units are used in the text with English equivalents in parentheses. Neither unit is uniformly accurate throughout because referenced units may have been either metric or English and because of rounding of numbers. Conversions of board feet to cubic meters, in particular, should be viewed as estimates rather than true measurements because of assumptions made in the conversion process.

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Acacia Koa A. Gray Koa

Leguminosae Legume family

Craig D. Whitesell

From the time of the early Hawaiians, koa (*Acacia koa*) has been prized for its exceptionally fine wood and is currently considered the most valuable of the common native timber species in Hawaii (*29,60*). Koa frequently has curly grain and striking coloration and has excellent working properties (*11,37,75*). It grows in nearly pure stands or in admixtures with ohia (*Metrosideros polymorpha*). Other tree species are sparse in these forests. A large evergreen hardwood tree endemic to the State, koa belongs to the thornless, phyllodinous group of the *Acacia* subgenus Heterophyllum.

Koa forests were more extensive in the past than they are today. Land clearing, poor cutting practices, and destruction by animals, insects (*49*), and fire (*26,36,67,96*) have all taken a toll. The volume of koa sawtimber totaled about 187 million board feet in 1970. At that time the commercial koa forest land in the State totaled about 7500 ha (18,600 acres), and commercial ohia-koa forests about 17 500 ha (43,200 acres). The estimated growing-stock volume of commercial koa exceeded 0.7 million m^3 (25 million ft^3) in 1978 (*50*).

Koa is an important component of montane Hawaiian rain forests. It is a nitrogen-fixing species. In dense, pole-size stands, nitrogen-rich koa foliage can account for 50 to 75 percent of the leaf-litter biomass produced annually (*68*). On the floor of cool mesic forests, koa phyllodes decompose rapidly; mean residence time has been estimated at 0.6 year (*68*). The abundance and distribution of the akiapolaau, akepa, and Hawaiian creeper, three of the endangered forest birds on the island of Hawaii, are strongly associated with koa in forest communities (*66*). Mature koa is needed for bird habitat: endangered birds do not use young, pure stands of koa, but do use the old, mixed-species stands adjacent to young stands (*65*).

Habitat

Native Range

The range of koa (fig. 1) extends from longitude 154° to 160° W.; its latitude ranges from 19° to 22° N. It is found on all six of the major islands of the Hawaiian chain: Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii.

Climate

Hawaii is tropical in latitude, with mild and equable temperatures at low elevations (table 1). Day length is nearly uniform year-round, varying by 2 hours. The northeasterly trade winds dominate; however, "Kona" storms from the south or west during winter, and occasional tropical storms throughout the year, bring high winds and heavy rains to the islands. Hawaii's mountains, especially massive Mauna Loa and Mauna Kea on Hawaii, and Haleakala on Maui, have a strong influence on the weather and provide climates ranging from the tropic to the subarctic (*7*).

Table 1—Mean temperature at five stations on the east flank of Mauna Kea, island of Hawaii[1]

Station	Elevation	Mean temperature	
		January	August
	m	*C*	*C*
Olaa (*6*)	85	21	24
Waiakea Forest	550	18	21
Waiakea Forest	915	17	19
Waiakea Forest	1220	13	16
Kulani Camp (*6*)	1580	4	14
	ft	*F*	*F*
Olaa	280	70	75
Waiakea Forest	1,800	64	69
Waiakea Forest	3,000	62	67
Waiakea Forest	4,000	55	61
Kulani Camp	5,190	39	58

[1] Data on file at the Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Honolulu, HI.

Rainfall varies greatly within short distances. Monthly amounts recorded over a period of years at weather stations in the koa belts show a phenomenal range. A Forest Service station at 1200 m (4,000 ft) elevation recorded a mean annual rainfall of 4300 mm (170 in) for a 14-year period, with extremes of 3450 to 5500 mm (136 to 216 in). During the driest month, only 19 mm (0.74 in) was recorded; the wettest month was 1380 mm (54.4 in).

Koa grows best in the high rainfall areas, those receiving 1900 to 5100 mm (75 to 200 in) annually. It also grows in areas that receive much less than this amount, but growth is slower and tree form is generally poorer. Cloud cover and fog commonly shroud the middle forest zone (600 to 1800 m or

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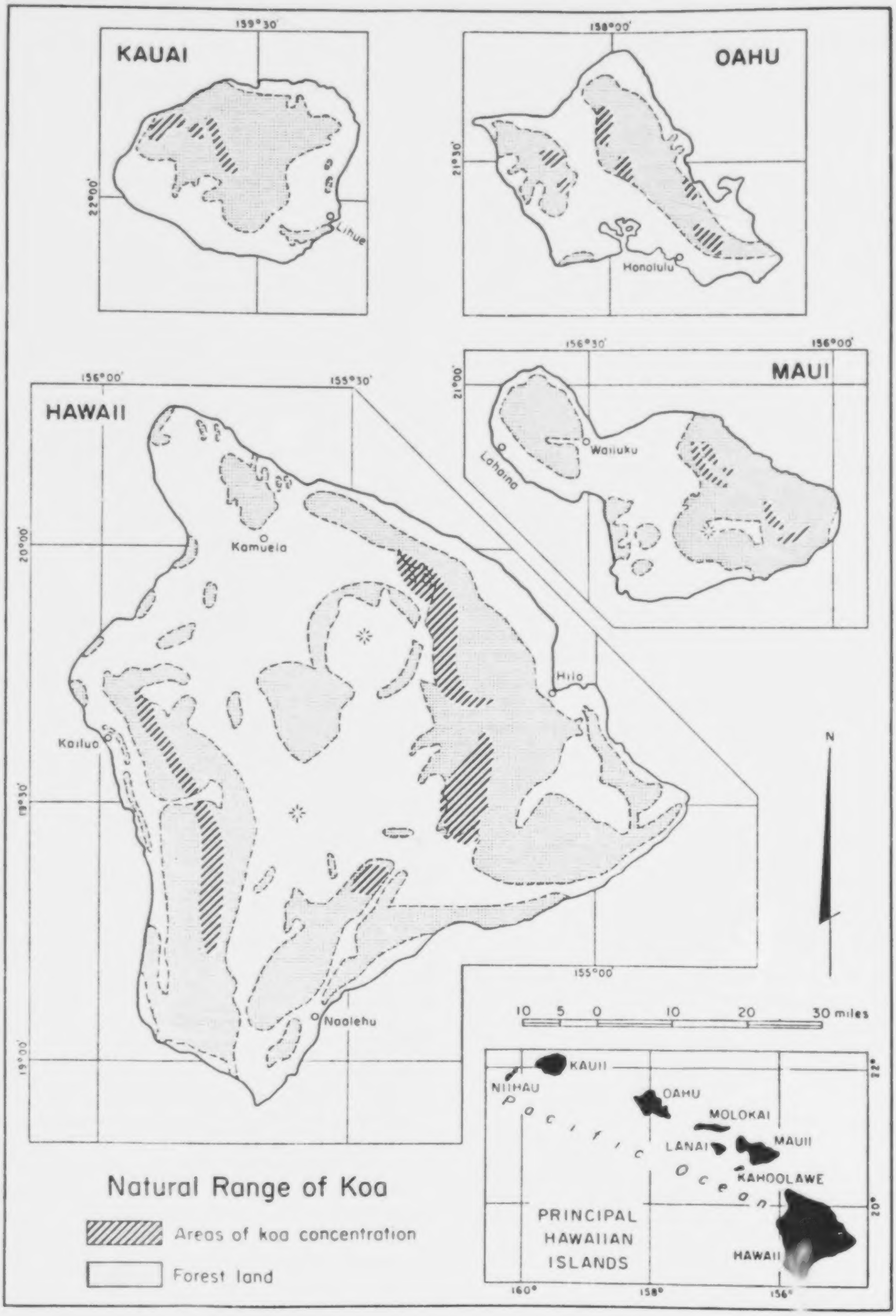
159°30'
KAUAI
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Lihue
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Honolulu
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MAUI
Wailuku
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HAWAII
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19°30'
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Naalehu
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N
10 5 0 10 20 30 miles
KAUII
NIIHAU
OAHU
MOLOKAI
LANAI
MAUII
KAHOOLAWE
HAWAII
Pacific Ocean
PRINCIPAL HAWAIIAN ISLANDS
22°
20°
160°
158°
156°
Natural Range of Koa
Areas of koa concentration
Forest land

Figure 1—*The native range of koa.*

2,000 to 6,000 ft) where commercial koa stands are concentrated. Frost is not uncommon during winter months above 1200 m (4,000 ft) elevation. Temperature ranges within the koa belt are small, as may be seen from data for Mauna Kea, island of Hawaii (table 1).

Soils and Topography

Koa is found on volcanic soils of all geologic ages and degrees of development, from the young ash and "aa" lava rock soils on the island of Hawaii to the oldest soils on Oahu and Kauai. The tree grows best on moderately well drained and well drained, medium to very strongly acid soils. These recent soils are higher in plant nutrients, having been subjected to less leaching and erosion than have the soils on the older islands.

Most koa forests grow on two of the great groups in the soil order Inceptisol: Hydrandepts and Dystrandepts. Hydrandepts are found in areas of high rainfall. They are high in amorphous materials and have high cation exchange capacities, but extremely low base saturations due to the high rainfall. Although deficient in available phosphorus, sodium, potassium, calcium, and silica, they have a high content of organic matter and hydrous oxides of iron and aluminum, manganese, and titanium. Infiltration rates are rapid and erosion is slight to moderate, depending upon the degree of slope. Dystrandepts are formed under lower rainfall than the Hydrandepts. They have slightly greater base saturations than the Hydrandepts.

The next most abundant soil great group on which koa grows is the well drained Tropofolists (organic soils of the order Histosols). Other minor soils include Haplohumults and Kandihumults of the order Ultisols and Hapludox and Acrudox of the order Oxisols.

Koa grows at elevations ranging from 90 m (300 ft) on Oahu *(45)* to 2100 m (7,000 ft) on Hawaii *(37)*, on flatlands and slopes. Koa has been listed as a component of the forests occupying gulch and ravine walls sloping 40 to 80° *(49)*. The flora of Hawaii have been divided into groups occupying different zones of elevation *(29)*:

The lowland zone, at or near sea level; open country, with isolated trees or clumps of trees. Koa rarely grows here.

The lower forest zone, upper limit 300 to 600 m (1,000 to 2,000 ft); tropical in character, woods rather open. Koa grows in scattered stands, in admixture with ohia.

The middle forest zone, upper limit 1500 to 1800 m (5,000 to 6,000 ft); within the region of clouds, where vegetation develops the greatest luxuriance. Here koa reaches its greatest development in size and number (fig. 2).

The upper forest zone, upper limit as high as 2400 to 2700 m (8,000 to 9,000 ft). Koa reaches into this zone, but seldom above 2100 m (7,000 ft).

Associated Forest Cover

Botanists and foresters have listed more than 80 trees, shrubs, vines, herbs, ferns, club mosses, grasses, and sedges associated with koa. Trees associated with koa *(20,33,48)* include:

'ahakea (*Bobea* spp.)
'ala'a (*Pouteria sandwicensis*)
kalia (*Elaeocarpus bifidus*)
kauila (*Alphitonia ponderosa*)
kawa'u (*Ilex anomala*)
kolea (*Myrsine lessertiana*)
kopiko (*Psychotria* spp.)
loulu palm (*Pritchardia* spp.)
mamani (*Sophora chrysophylla*)
naio (*Myoporum sandwicense*)
'ohe'ohe (*Tetraplasandra hawaiiensis*)
'ohi'a (*Metrosideros polymorpha*)
'olapa (*Cheirodendron trigynum*)
olomea (*Perrottetia sandwicensis*)
olopua (*Osmanthus sandwicensis*)
pilo (*Coprosma* spp.)
sandalwood (*Santalum* spp.)

Life History

Koa is a phyllodial species that undergoes a change from true leaves (consisting of 12 to 15 paired, bipinnate leaflets) to sickle-shaped phyllodes (dilated petioles). In most cases where light is sufficient, the change occurs while plants are smaller than saplings, i.e. < 2 m (6 ft) tall. Investigations suggest that true leaves promote more rapid early growth when moisture is adequate, whereas, during periods of drought, phyllodes are better adapted *(27)*. Phyllodes persist under moisture stress, transpiring about 20 percent as much as true leaves, and their stomata close four times faster after dark *(97)*. Old trees usually bear only laurel green phyllodes, but sometimes true leaves appear on the trunk or lower branches, or after wounding.

Reproduction and Early Growth

Flowering and Fruiting—The flowers of koa are borne over the outer part of the crown. Seedlings have been observed in flower and fruit *(3,80)* at 2 and 3 years of age. One of the pollinating insects found on koa flowers is the honeybee (*Apis mellifera*). The extent to which other insects, birds, and wind affect pollination is not well documented. Koa initiates flower development nearly year-round at the high elevation on Mauna Loa, reaching a peak during the wet season in late winter (*46*). On adjacent Mauna Kea, koa flowers appear from December through February, with few flowers at any other time. At lower elevations, on all of the islands, flowering usually occurs from late winter to early summer (July). Weather conditions, especially severe droughts, influence the timing and extent of flowering at any time of the year.

The inflorescence of koa is an axillary raceme of pale yellow heads averaging 8.5 mm (0.3 in) in diameter (*29*), one to three on a common peduncle, and composed of many hermaphroditic (bisexual) flowers. Each flower has an indefinite number of free stamens and a single elongated style. The heads are highly dichogamous, with anthers dehiscing 3 to 8 days before the stigmas are fully exserted (*8*).

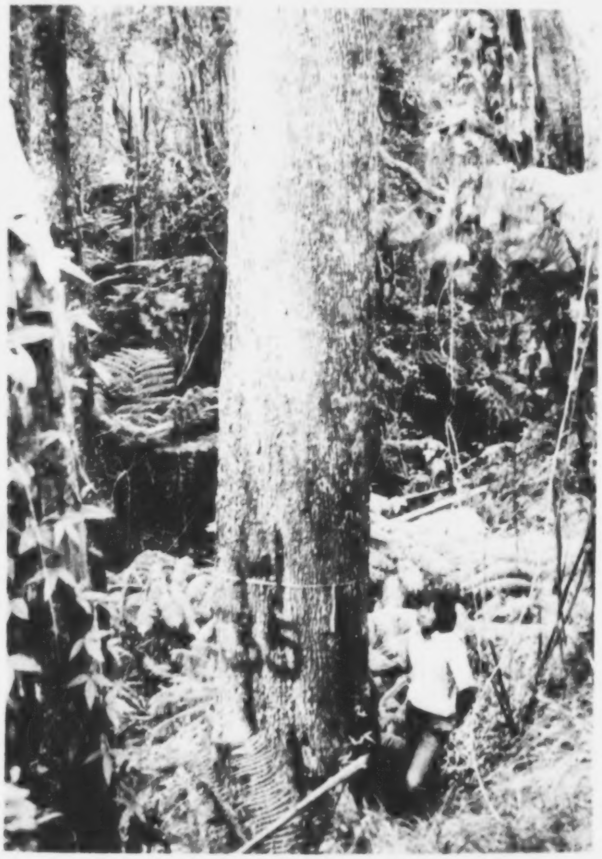

Figure 2—*A superior koa tree chosen for seed collection, island of Hawaii.*

The fruit is a legume, slow to dehisce, about 15 cm (6 in) long and 2.5 to 4 cm (1 to 1.5 in) wide. The pods contain about 12 seeds that vary from dark brown to black. They mature at different times throughout the year, depending on location and weather conditions.

Seed Production and Dissemination—No records of the frequency of exceptionally good or poor seed years are available, but seed years do vary.

Koa seed pods dehisce while on the tree or fall to the ground unopened, where they either dehisce or disintegrate. "The horny seed often remains on the tree for a year after it ripens, and when lying on the ground is known to have retained for a period for 25 years its ability to germinate" (*37*). Koa seeds are seldom dispersed far beyond the crown, but, occasionally, wind may carry unopened pods some distance. Seeds from koa growing in gulches may be carried downstream to lower elevations, especially during torrential rains.

Koa seeds, like those of other acacias, are among the most durable of tree seeds and need not be kept in sealed containers. They will germinate after many years of storage if kept in a cool, dry place. The seeds have hard coats that retard germination unless they are first mechanically scarified, briefly treated with sulfuric acid, or soaked in hot water. The water treatment is the most practical. The seeds are placed in nearly boiling water, after the heat source is removed, and allowed to soak for 24 hours. Seeds that fail to swell the first time may again be subjected to this pregermination treatment, often with success (*99*). In seven samples, the number of clean seeds ranged from a low of 5,300/kg to a high of 16,300/kg (2,400 to 7,400/lb).

Seedling Development—The mode of germination is epigeal (*99*). Light is not a requirement for germination (*83*). Under favorable conditions—bare mineral soil, adequate moisture, and exposure to sunlight—koa seedlings will grow readily. Soil aeration and soil temperature may influence germination (*83*).

Until recent years, the standard nursery practice was to sow koa seeds in wooden flats, then transplant the seedlings to tin cans (*35*). Now, plastic bags or tubes are used. Tube-grown seedlings are easier to plant.

Properly pretreated koa seeds should be covered with 6 to 12 mm (0.25 to 0.5 in) of soil; they begin to germinate within a week. Seedlings in bags or tubes can be grown to plantable size of 20 cm (8 in) high in 10 to 14 weeks.

Direct seeding of koa on prepared seed spots has been moderately successful *(9,13)*. In two trials comparing broadcast sowing with direct sowing into prepared spots, stocking was four times higher on the direct seeded spots on Maui, whereas no difference in the percentage of stocked spots or of height growth was evident on the island of Hawaii.

Koa has been recommended for watershed planting on well drained areas *(34,37,39)* and is described as "the one native tree which can be easily handled in nursery and planting operations...suitable for the larger portion of areas in need of reforestation and particularly for the drier ridges and slopes" *(35)*.

Other investigators, less enthusiastic about planting koa, did not recommend it *(13,17)*, commenting as follows: "Results on older soil formations have been uniformly disappointing. Frequently, the trees die out after 15 to 20 years" *(17)*. Plantations established on Maui during the late 1930's developed scattered, large trees of exceptionally poor form. Relatively few koa seedlings were planted after World War II. However, in the past 10 years, private land owners on the island of Hawaii, influenced by the short supply, began planting koa *(104)*.

Seedlings usually appear soon after land is cleared for pasture or roads, or after fires. As many as 354,700 koa seedlings per hectare (143,537/acre) were counted in the vicinity of old koa trees in burned-over areas *(41)*. Seeds escaping the flames may be induced to germinate by the heat.

Koa seedlings grow rapidly. One month after a burn, koa seedlings were at least 2.5 cm (1 in) tall; after 3 months they ranged from 10 to 28 cm (4 to 11 in) tall, averaging about 13 cm (5 in) *(41)*. On a cleared area at 500 m (1,700 ft) elevation, 1-year-old seedlings ranged from 0.6 to 4 m (2 to 13 ft) tall and averaged 2 m (6 ft). On favorable sites, seedlings attain 9 m (30 ft) in 5 years *(37)*. Eight months after a fire on Kauai, koa regeneration was most common near fire-killed parent trees, and maximum height growth was 4.6 m (15 ft) *(103)*. The abundance, distribution, growth, and mortality of koa on burned-over areas on Oahu were monitored over a 2.5-year period *(73)*. During this time, seedling density declined dramatically. The root-crown fungus *Calonectria crotalariae* caused more than half of this mortality. On these sites the seedlings grew about 2.3 cm (1 in) per month. Koa did poorly when planted on abandoned sugarcane land on the windward coast of the island of Hawaii. Survival at age 6 years was 78 percent, but trees averaged only 3 m (10 ft) tall and only 62 percent were judged vigorous. Tree form varied from good to poor, with 77 percent cull *(101)*.

The abundance and distribution of natural regeneration after logging were studied on a 200-ha (500-acre) tract heavily infested with pigs and vines on the island of Hawaii *(70)*. Seedling density of koa was about three times as great in disturbed as in undisturbed areas. Most koa seedlings found on the ground disturbed by logging were well established, but none of those growing on undisturbed ground were large enough to have much chance of surviving the menacing pigs and cattle. Koa seedlings in disturbed areas tend to be clustered around seed trees *(70)*. In 1922, Krabel stated: "Where cattle have been excluded for a number of years, koa groves are developing with surprising speed on exposed and barren ridges" *(43)*.

The stimulating effect of soil scarification on seedling emergence is helpful in regenerating koa on degraded forest land where seed reserves still exist in the soil. Disking in the sparsely wooded pastures of the Hakalau Forest National Wildlife Refuge resulted in koa reproduction. Even in open areas far removed from live or skeletal remains of koa, a few seedlings emerged *(15)*.

In the natural rain forest, koa seedlings can emerge from mineral soil and organic seedbeds, such as decaying logs and treefern trunks. Seedling growth is generally slower on old logs than on mineral soil, possibly due to low nutrient availability. However, seedlings tend to survive better on organic seedbeds because these sites are elevated and out of reach of feral pigs. In the Kilauea Forest, more than 60 percent of the mature koa initially emerged from logs or other large organic seedbeds *(16)*. Nevertheless, rarely do koa seedlings survive in the dense rain forest unless openings have been created, as by windthrow. Gap-phase replacement seems to be the primary mechanism by which koa is maintained in natural rain forest communities *(53)*. Serious disturbances, such as fire or hurricane-induced windthrow, typically stimulate large-scale koa reproduction.

Vegetative Reproduction—An intensive study of koa reproduction was made in 1943 *(5)* in an area of the Volcanoes National Park on the island of Hawaii, where annual rainfall is about 1000 mm (40 in). Koa stands appeared to regenerate almost entirely by means of root suckers on this once heavily grazed site. The researchers reported that "many vigorous suckers arise from the buried and exposed roots of a single tree. In three cases, suckers were seen 15, 27, and 29 m (50, 90, and 95 ft) away from the base of isolated koa trees. Suckers developed into healthy trees 8 to 16 cm (3 to 6 in) in diameter breast height in 5 to 6 years and were estimated to be 4 m (12 ft) tall." Koa colonies (root sprouts originating from the mother tree) in the park expanded at the rate of 0.5 to 2.5 m (1.5 to 8 ft) per year *(51)*. In 1973, a study to determine the influence of feral goats on growth of these root suckers found that the suckers became more numerous and vigorous once the goats were excluded *(84)*. Suckering, however, did not occur where the soil was covered with tall dense grass *(83)*.

Koa can be propagated by rooting of cuttings under mist and shade when the material is in the immature, true-leaf stage of growth. Air layers of root suckers gave 16 percent rooting success, but rooting of root sucker cuttings under mist was highly variable, generally with a 20 percent success rate *(76)*. Koa can be also propagated by callus cultures derived from shoot tips, but the method is slow and labor-intensive and not presently adaptable to large scale propagation *(79)*. However, one clone, comprised of hundreds of ramets, has been produced by tissue culture of seedling shoot-tip callus *(81)*. These tissue-cultured trees have been successfully outplanted in progeny tests *(82)*.

Koa root sprouts are common in rain forests as well as in savanna stands. Efforts to induce suckering of roots of selected plus trees, in situ, on both wet and dry areas failed, however. Attempts to simulate the actions of pigs and cattle with treatments including knife wounding, "chewing" with pliers, pounding, and exposure had no effect. Koa root suckers in rain forests are much more common on roots in deep shade or hidden under dense grass than in roots exposed to direct sunlight *(76)*. Stump sprouts have rarely been observed but do occur.

Sapling and Pole Stages to Maturity

Growth and Yield—Age of koa trees cannot be determined. Growth rings were not correlated with "annual rings" *(102)*. Old relic forests still in existence were probably present at the time Captain James Cook discovered the Hawaiian Islands in 1778. The largest koa tree on record had a d.b.h. of 363 cm (143 in), total height of 43 m (140 ft), and a crown spread of 45 m (148 ft) *(56)*.

Stocking and growth data for natural regeneration on heavily disturbed sites and one plantation on the island of Hawaii are available (table 2).

The form of koa varies greatly. Most mature trees have large, open, scraggly crowns with limby, fluted boles. In the rain forests, on deep, rich soil, an occasional koa tree may surpass 34 m (110 ft) in height, but few possess clean, straight boles. On drier sites, the form of koa is even poorer, and trees are often stunted and misshapen. Precise yield figures from koa stands are not available.

Missing from the koa and ohia-koa forests in many areas are the koa-size classes that normally form the recently mature, vigorous stands. In 1913, the condition of large tracts of koa forest was graphically described by Rock *(62)*:

"Above Kealakekua, South Kona, of the once beautiful koa forest, 90 percent of the trees are now dead, and the remaining 10 percent in a dying condition. Their huge trunks and limbs cover the ground so thickly that it is difficult to ride through the forest, if such it can be called.... It is sad, however, to see these gigantic trees succumb to the ravages of cattle and insects."

Forest survey data from 1959-61 *(98)* indicated the condition of much of the sawtimber-size koa (trees more than 27.7 cm [10.9 in] in d.b.h.). Of 103 trees classified according to merchantability on the basis of form and defect, 36 percent were merchantable, 15 percent sound cull (with such defects as crook, excessive limbs, or poor form), and 49 percent rotten cull (excessive rot). Of the 103 trees, the average d.b.h. was 89 cm (35 in); of 31 trees, the average height was 22 m (72 ft), and the average crown diameter was 18 m (58 ft). Log grades were determined for logs in 103 koa trees. Less than two-fifths of all butt logs (first 4.9 m [16 ft]) met the specifications for either factory lumber logs or tie and timber logs. More than three-fifths were cull. Only 35 percent of the 103 trees sampled had an upper log of 2.4 m (8 ft) or more, and more than half of these logs were graded cull *(98)*. Remeasurements in 1969-70 of the plots inventoried 10 years earlier *(54)* permit esti-

Table 2—Characteristics of koa growing in three natural stands and a plantation in Hawaii[1]

Location	Annual rainfall	Age	Stand stocking	Dominants	
				D.b.h.	Height
	mm	*yr*	*stems/ha*	*cm*	*m*
Natural stands					
1	3810	8	3460	12.7	6.0
2	5080	17	790	23.1	17.4
3	2540	15	2720	18.5	13.1
Plantation	3810	27	395	31.0	14.4
	in	*yr*	*stems/acre*	*in*	*ft*
Natural stands					
1	150	8	1,400	5.0	19.6
2	200	17	320	9.1	57.0
3	100	15	1,100	7.3	43.0
Plantation	150	27	160	12.2	47.3

[1] Ching, Wayne F. 1981. Growth of koa at selected sites on the island of Hawaii. Unpublished report. Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife, Honolulu, HI. 10 p.

mates of annual growth and mortality of koa on the island of Hawaii. Net annual growth was found to be a negative 4.52 million board feet of sawtimber and a negative 15 660 m^3 (553,000 ft^3) of growing stock *(50)*. One study offers guidelines for estimating the volume of unsound wood associated with log surface defects common in koa *(12)*.

Rooting Habit—Little is known of the root development of koa. The tree grows on the deep Hawaiian soils, but also reaches impressive size on the shallow "aa" lava flows. "The root system of the mature koa is shallow and extensive, spreading out radially from the base for distances as great as 30 m (100 ft) or more" *(5)*. "The tree has a shallow rooted system, a flat plane of roots spreading out in all directions just beneath the surface of the ground. For this reason the larger top-heavy trees are easily overturned by severe windstorms...." *(37)*. Large koa trees were toppled during a severe earthquake on the island of Hawaii in 1973. In describing the root systems of lava-flow plants, a researcher classified koa as one of the comparatively deep-rooted woody species *(48)*.

Reaction to Competition—Koa is classed as intolerant of shade both in the dry forest *(28)* and in the rain forest, and at all ages *(26)*. Under favorable light, moisture, and soil conditions, koa competes aggressively with other vegetation.

Koa has been classified in various ways by different investigators. One referred to koa as a pioneer species on the grassy slopes of dry forest sites *(28)*, but another considered it a climax species *(21)*. Koa has been considered the ultimate forest type, following the ohia forest on the ancient "aa" lava flows *(37)*. "At maturity a grove (of koa) casts a shade in which its own seedlings have difficulty in growing, and unless they fill a vacancy in the parental ranks, they must seek the outer limits of the stand" *(64)*. Another investigator believed that koa "reproduction need not be especially frequent to maintain the forest (type)" *(45)*.

Koa failed when underplanted in a dense native ohia rain forest at 870 m (2,850 ft), showing poor survival (44 percent), vigor, and form (70 percent cull), but three introduced nonleguminous species from Australia performed well *(100)*.

The effect of thinning and/or fertilizing a 12-year-old, stagnated koa stand were studied on the island of Maui. In this precommercial thinning, the number of stems was reduced 50 percent. Basal area growth rates for a 3-year period indicated that thinning increased growth significantly. Fertilizer yielded limited response; and the investigator thought that the fertilizer should be applied before crown closure *(72)*.

Damaging Agents—Hawaiian forestry literature is full of references to the disastrous effects of cattle, pigs, sheep, and goats on koa and other native species *(1,4,5,17,26,35,38,40,77)*. Records of the Hawaii Division of Forestry and Wildlife show that more than 250,000 pigs, goats, and sheep were destroyed from 1921-46 in the forests of the island of Hawaii *(10)* during an eradication program. Such efforts did much to reduce the amount of browsing by these animals on koa forests. Feral cattle are particularly fond of koa root sprouts, seedlings, pods, and leaves. They straddle and trample large saplings to devour the foliage and bark. Feral goats have nearly disrupted the replacement cycle of koa on the Hawaii Volcanoes National Park *(84)*. In recent years, park rangers have taken steps to radically reduce the size of the goat herds within the park. A study was conducted on the recovery of vegetation on koa parklands on Maui following the exclusion of goats. After 7 years, young koa regeneration was present both within and outside the enclosure, but the koa got large only if the goats were excluded *(69)*. Koa will recover on these parklands if goats are eliminated. A large number of feral pigs inhabit the koa rain forests, and their rooting destroys many koa seedlings. It is thought that if the pig population is permitted to increase, the koa rain forest ecosystem will deteriorate *(16)*.

Koa attracts other kinds of animals. Black-tailed deer, introduced from Oregon to the island of Kauai in 1961, eat koa seedlings, but have little impact on the native vegetation. Less than 10 percent of the koa was browsed *(94)*. The tree rat and the Hawaiian rat damage koa saplings by stripping off bark. One thousand koa saplings (2 to 5 years old) along an elevation transect from 770 to 1330 m (2,520 to 4,370 ft) in the Laupahoehoe area of the Hilo Forest Reserve were examined *(71)*. Thirty percent of the trees had been wounded by rats, with wounds occurring as high as 10 m (33 ft). Bark along the main trunk and on lateral branches was subject to stripping. Terminal and lateral shoot dieback were observed where complete girdling occurred. In a study of mortality of koa saplings severely wounded by rats, damage was reported most severe in the vicinity of brush piles where nests were likely to be located.

In 1925, more than 40 species of native insects were considered enemies of koa *(92)*, and by 1983 the number of phytophagous insects associated with koa reached 101 *(87)*. Insect damage to koa is well documented *(18,22,58,59,91)*. One authority believes "there are more endemic insect species attached to this koa complex (*Acacia koa* and related koa members) than to any other genus in the Hawaiian islands" *(93)*.

One of the most destructive insects of koa is the koa moth (*Scotorythra paludicola*), a lepidopterus defoliator found on the islands of Hawaii, Maui *(105)*, Oahu, and Kauai *(87)*. Severe outbreaks occur periodically. When these insects appear in large numbers, they may completely defoliate koa stands. Following an outbreak on Maui in which 1841 ha (4,550 acres) were completely defoliated, growth was reduced 71 percent, and about one-third of the trees died within 20 months *(88)*.

The introduced koa haole seed weevil (*Araecerus levipennis*) is the most prevalent insect that infests koa seeds, the next most common being *Stator limbatus* *(85)*. The koa seedworm (*Cryptophlebia illepida*) destroys seeds and is a problem to control when seeds are collected for reforestation purposes. Eighty percent of the damage from this Tortricid occurs above 1037 m (3,400 ft) *(85)*. Three other Tortricid species destroy koa pods or seeds *(85,91)*. These seed moths may destroy 90 percent or more of any given seed crop in the pods *(93)*. Stein *(86)* reviewed the biology and host range of koa seed insects, their parasites, and hyperparasites.

At high elevations, koa terminals are sometimes heavily attacked by the Fuller rose beetle (*Pantomorus cervinus*), but the attacks appear to be highly seasonal and of no serious consequence. The acacia psyllid (*Psylla uncatoides*), first found in Hawaii in 1966, feeds and breeds in the new growth of koa. This psyllid also has become a serious pest of the closely related koaia (*Acacia koaia*) *(47)*. The black twig borer (*Xylosandrus compactus*) is associated with injury and mortality.

Information on diseases of koa has increased in recent years. Seedlings may be attacked by *Calonectria theae*, which causes a shoot blight *(55)* and *C. crotalariae*, which causes a crown rot *(57)*. This pathogen also caused a collar rot that severely affected koa seedlings regenerating a burned-over area *(2)*. A wilt disease, *Fusarium oxysporum*, was observed among koa seedlings *(24)*. This fungus may contribute to the premature decline or death of old koa trees growing within the Hawaii Volcanoes National Park. Indications are that this fungus is seedborne, but seed disinfection did not reduce disease incidence *(24)*. Koa was moderately tolerant to *Phytophthora cinnamomi* in greenhouse tests *(42)*.

Dieback is common in the crowns of old trees, and it was observed in more than half the sawtimber-size koa measured during the 1959-61 forest survey. The root-rot fungus *Armillaria mellea* is associated with this dieback *(44,61)*. Stands possibly weakened by old age, extended droughts, and grazing have succumbed to attacks by this fungus. Other diseases of koa are those caused by the sooty molds, such as *Meliola koae* that cover the leaves and restrict growth.

Four rust fungi, *Uromyces koae*, *U. digitatus*, *Endoraceium acaciae*, and *E. hawaiiense*, occur on koa *(25,32)*. Both species in the genus *Uromyces*, obligate parasites, cause witches' brooms and leaf blisters that deform branches and phyllodes. When infections are heavy, they can deform and debilitate both young and old trees *(23,30,31)*.

The Hawaiian mistletoe (*Korthalsella complanata*) has been observed in many koa stands, and it can deform young koa. Heart rot, caused principally by *Laetiporus sulphureus* and *Pleurotus ostreatus*, is common in most mature and overmature koa *(6)*. More than half the large koa measured in the 1959-61 forest survey were unmerchantable because of excessive rot *(98)*.

Pole-size and small, sawtimber-size koa have thin bark and are easily damaged by fires.

Weeds are serious problems in certain areas. The banana poka (*Passiflora mollissima*) smothers both koa reproduction and mature trees by laying a curtain of vines over them. The German-ivy (*Senecio mikanioides*) is also difficult to control.

Special Uses

The most important use of koa timber by the Hawaiians was to build canoes. The largest of the giant war canoes extended 21 m (70 ft). Canoe hulls were made of single, giant koa logs. Koa was also used for surfboards, some 5.5 m (18 ft) or longer, for paddles, and for framing grasshouses. The bark provided dye to tapa, a light cloth made from the bark of wauke (*Broussonetia papyrifera*) *(11,19)*.

Koa wood is now used primarily for furniture, cabinet work, and face veneers. It is widely used in woodcraft. Cabinet makers recognize a dozen or more types of koa wood, including curly or "fiddle back" koa, red koa, and yellow koa *(11)*. One local use is for making ukuleles. At one time koa was sold on the world market as Hawaiian mahogany *(62)*.

Large logs have a narrow, creamy-white band of sapwood. The heartwood may vary through many rich shades of red, golden brown, or brown. The heartwood seasons well without serious degrade from warping, checking, or splitting *(74)*.

Although it has been stated that foresters in Hawaii have paid little attention to koa *(83)*, more than 1.3 million koa seedlings were planted by the Hawaii Division of Forestry and Wildlife between 1915 and 1946 *(78)* for watershed protection. Koa, however, did not perform as well as many introduced species on these deteriorated sites.

Genetics

Morphological differences in koa have been observed on several islands. In 1920, Rock *(63)*, named two varieties: *Acacia koa* var. *lanaiensis* (Hillebrand's A. *koa*-B var.) and *A. koa* var. *hawaiiensis*, after the islands on which they were found. Ecotypic variation can be found from island to island. Studies of such variation are complicated by past plantings of mixed seed lots collected throughout the islands; such mixed plantings could now be hybridizing.

Collections of the koa group, all commonly referred to as koa, were studied, and in 1979 this classification was presented by St. John *(90)*:

Acacia koa var. *koa*, grows on the six larger islands.

Acacia koa var. *waianaeensis* grows only on Oahu, and most commonly in the Waianae Mountains.

Acacia koa var. *latifolia*; syn. *A. koa* var. *hawaiiensis* Rock, grows on the island of Hawaii in the rain forest, and at higher elevations on the more open ranch and park land. Altitudinal races of koa probably exist *(52)*.

Two other native species related to koa are recognized. On western Kauai, one of the oldest Hawaiian Islands, a form of acacia is found that differs from koa in sepals, petals, inflorescence *(63)*, and seed shape *(37)*. This species, also called koa, is *Acacia kauaiensis*. A second species closely related to koa is koaia *(A. koaia)*, a narrowly distributed, small, shrubby tree occupying dry, leeward sites below 1050 m (3,500 ft) on Molokai, Maui, and Hawaii *(89)*. *Acacia koaia* differs from koa in the shape of the pods and phyllodes *(63)*. The native and introduced species of *Acacia* found on Lanai have been described *(20)*.

Other *Acacia* species related to koa are found outside of Hawaii. *Mascarene acacia* (*A. heterophylla*) is endemic to Reunion island and Mauritius island, both about 725 km (450 mi) east of Madagascar, in the Indian Ocean. It is so similar to koa that the trees were initially identified as the same species. The two were identified by another botanist as separate species, however, entirely on the basis of distance and isolation. In 1969, significant differences were found in fruit and seed size, corolla structure, and morphology of the first two leaves of the two species *(95)*.

Tasmanian blackwood (*Acacia melanoxylon*), native to Australia but planted in many countries, resembles koa. It has straighter and shorter phyllodes, a narrower curved pod, a more pointed crown *(63)*, but similar wood. Another closely related species, *A. simplicifolia*, grows in Samoa, New Hebrides, New Caledonia, and Fiji *(20,59,60)*.

In 1948, one investigator determined that koa is a tetraploid with 2n = 52 and stated that all other phyllodinous acacias studied have the diploid chromosome complement *(3)*. He reasoned "that polyploidy in *Acacia koa* occurred after the initiation of phylloidy. This is supported by its distribution as an endemic island extension of the Australian flora." In 1978, koa was observed to have a gametic number of 26, verifying that it is tetraploid *(14)*. Another investigator *(95)* reported on the work of Lescanne, who observed that the closely related *A. heterophylla* was also a tetraploid, with 2n = 52.

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Acer barbatum Michx. Florida Maple

Aceraceae Maple family

Earle P. Jones, Jr.

Florida maple (*Acer barbatum*), also called southern sugar maple and hammock maple (*8*), is a minor, mostly understory species. Specific information about many features of this species is lacking, but it is similar in most respects to sugar maple (*A. saccharum*). Champion-sized trees have been found in Alabama and South Carolina measuring 86 and 71 cm (34 and 28 in) in d.b.h.; 34 and 38 m (110 and 126 ft) in height (*4*).

Habitat

Native Range

The range of Florida maple (fig. 1) is discontinuous in the Piedmont and Coastal Plain from southeastern Virginia southwest across North and South Carolina and Georgia, into the Florida Panhandle. The range continues west across Alabama, Mississippi,

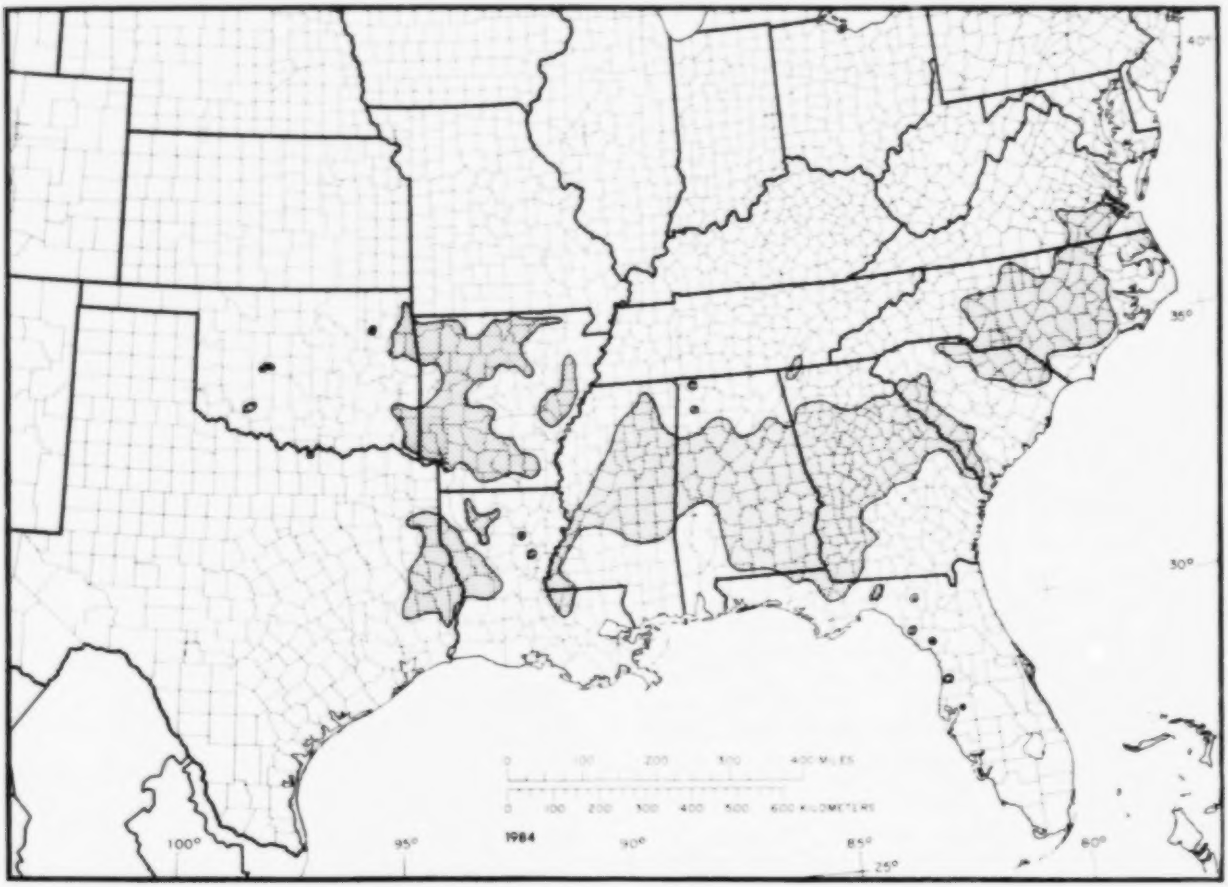

Figure 1—*The native range of Florida maple.*

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Louisiana, into eastern Texas, and north across Arkansas into eastern Oklahoma. The species is also found in isolated spots halfway down the Gulf Coast of the Florida peninsula and at one location in central Oklahoma *(8)*.

Climate

Across the range of Florida maple, average annual rainfall varies from about 1120 to 1630 mm (44 to 64 in). Precipitation is well distributed, with the driest months averaging no less than 50 mm (2 in). January normal daily temperatures across the species' range vary from 11° to 18° C (52° to 64° F) maximum, and from -2° to 7° C (28° to 45° F) minimum. July normal highs are 29° to 33° C (84° to 91° F), and lows are 21° to 24° C (70° to 75° F). The average frost-free season is approximately 200 to 270 days *(11)*.

Soils and Topography

Florida maple grows on fertile, moist but well-drained soils on stream terraces, in coves, and on adjacent bluffs and ridgetops. It usually grows best on soils underlain by calcareous material such as limestone or marl. It also grows well on the Florida hammocks. Soils commonly are found in the orders Inceptisols, Entisols, and Ultisols.

Associated Forest Cover

Florida maple has not been included as an associate in any of the published descriptions of forest cover types. It is often ranked as a major component of the understory stand, however *(1)*. Associated overstory species include sweetgum *(Liquidambar styraciflua)*, willow oak *(Quercus phellos)*, cherrybark oak *(Q. falcata* var. *pagodifolia)*, winged elm *(Ulmus alata)*, red maple *(Acer rubrum)*, yellow-poplar *(Liriodendron tulipifera)*, ash *(Fraxinus* spp.), water oak *(Quercus nigra)*, and sugarberry *(Celtis laevigata)*.

Understory associates include American elm *(Ulmus americana)*, dogwood *(Cornus florida)*, possumhaw *(Ilex decidua)*, winged elm, American hornbeam *(Carpinus caroliniana)*, eastern redcedar *(Juniperus virginiana)*, red mulberry *(Morus rubra)*, northern red oak *(Quercus rubra)*, pignut hickory *(Carya glabra)*, and white ash *(Fraxinus americana)*.

In Florida, associates are basswood *(Tilia caroliniana)*, sweetgum, cabbage palmetto *(Sabal palmetto)*, water oak, willow oak, southern red oak *(Quercus falcata* var. *falcata)*, and loblolly pine *(Pinus taeda)*. Spruce pine *(P. glabra)* is an associate in Alabama *(6)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Florida maple is polygamo-dioecious. Flowers are small and are borne on long, puberulent pedicels in yellowish-green corymbs *(12)*. They appear as small clusters at the ends of branches and mature in the early spring, before or with the leaves *(3,13)*, usually in late March and April, about 2 weeks before sugar maple in the same vicinity.

The fruit is a winged, green to reddish, double samara, smaller than that of sugar maple, and matures in early summer. There are no seed test records

Figure 2—*Florida maple in Florida Caverns State Park in northwest Florida.*

for Florida maple on file at the National Tree Seed Laboratory at Macon, GA *(5)*.

Seed Production and Dissemination—Florida maple has not been managed as a commercial timber species and no published reports of seed production, dissemination, or experience in forest or nursery regeneration are available. The method of propagating Florida maple from seed is similar to that for sugar maple *(12)*. Germination is epigeal *(10)*. Reproduction of Florida maple has been described as erratic and scattered, occurring singly and in small groups *(9)*.

Seedling Development—No information available.

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—Because Florida maple (fig. 2) is primarily an understory tree, it is usually smaller and more spreading than sugar maple. A bottomland forest near Durham, NC, contained 23.5 percent Florida maple stems in the understory and 1.4 percent in the overstory *(1)*. Recent inventories by the Southeastern Forest Experiment Station *(2)* show that in the five southeastern States, Virginia, North Carolina, South Carolina, Georgia, and Florida, 91 percent of the Florida maple trees on commercial forest land are smaller than 13 cm (5 in) in d.b.h., and only 1 percent are 28 cm (11 in) in d.b.h. and larger. Total inventory of commercial Florida maple trees 13 cm (5 in) d.b.h. and larger in the 5-State area is 1,702,000 m^3 (60,134,000 ft^3) and of this volume 60 percent is in Georgia and Florida. Florida maple has a "medium" growth rate, meaning that dominant and codominant trees on better sites average 5 to 8 cm (2 to 3 in) of diameter growth over a 10-year period *(9)*. A composite of reports indicates that a mature Florida maple in the overstory may average 61 cm (24 in) in d.b.h. and 12.2 to 18.3 m (40 to 60 ft) in total height.

Rooting Habit—No information available.

Reaction to Competition—Florida maple is tolerant of shade *(9)*. There are no reports of how Florida maple responds to release or other silvicultural treatments.

Damaging Agents—Florida maple suffers no special damage problems *(9)*, and perhaps it can be assumed that generally the same insects and diseases that attack sugar maple also attack Florida maple, because the two species are so similar *(10)*.

Special Uses

Although Florida maple is not managed as a commercial species, it is used with associated commercial species for pulpwood, sawtimber, and veneer stock. It is included in the hard maple group and better trees may be used for furniture, flooring, paneling, and shoe lasts *(12)*, although its scarcity, small size, and poor form limit it to occasional use for factory and box lumber *(9)*. It has found considerable use in urban forestry as an ornamental or shade tree. Florida maple is a limited source of maple syrup.

Genetics

There has been considerable confusion in the classification of Florida maple as a species distinct from sugar maple, and in the field, Florida maple is probably often confused with other maples *(9)*.

Florida maple has been variously recognized among authorities as southern sugar maple *(Acer floridanum)* and as a sugar maple variety *(Acer saccharum* var. *floridanum)*. However, the distinction between (northern) sugar maple and Florida maple is based on the latter's smaller leaves with short, acute lobes, smaller samaras, and a more whitish bark *(12)*. Numerous intergrades between the two species have been found in east Texas and in the zone from Maryland south to northern Florida (although Maryland is not included in the range of *A. barbatum*). It appears that genes of both taxa are present in this intermediate population from Maryland to Florida and limited gene exchange is still occurring where one or the other taxon comes in contact with the intermediates *(7)*.

The literature contains no specific information about Florida maple hybrids, but in view of its close association with sugar maple, and the intergrades between the two species already mentioned, it is not unlikely that hybridization between the two species may occur.

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Acer macrophyllum Pursh Bigleaf Maple

Aceraceae Maple family

Don Minore and John C. Zasada

Bigleaf maple *(Acer macrophyllum)*, also called broadleaf maple or Oregon maple, is one of the few commercial hardwood tree species on the Pacific Coast. It is small compared with its conifer associates. Most mature bigleaf maples are about 15 m (50 ft) tall and 50 cm (20 in) in d.b.h. *(5)*. Large trees often reach heights of 30 m (100 ft) and diameters of 90 to 120 cm (36 to 48 in). True to its common name, bigleaf maple usually bears leaves up to 30.5 cm (12 in) across, and exceptionally large leaves may attain widths of 61 cm (24 in) *(2)*. They are borne on rounded crowns supported by short, branching boles if open-grown, but trees growing in dense stands are often well formed and free of branches for half to two-thirds of their height (fig. 1). Bigleaf maple is an excellent shade tree. The wood is used for furniture, especially piano frames, and the sap can be made into syrup.

Habitat

Native Range

The native range of bigleaf maple (fig. 2) extends from latitude 33° to 51° N., always within 300 km (186 mi) of the Pacific Ocean. This maple is not found in southeastern Alaska or on the Queen Charlotte Islands *(34)*, but it does grow on Vancouver Island at least as far north as Port Hardy *(25)*. On the mainland, the range is a continuous belt from near Sullivan Bay, BC, to within 16 km (10 mi) of San Francisco Bay, CA—a belt that includes the western slopes of the Coast Ranges of British Columbia, the Olympic Peninsula in Washington, the Coast Ranges of Oregon and California, and the western slopes of the Cascade Range in Oregon and Washington. The species is less common south of San Francisco Bay, but extensive stands are found in the Santa Cruz and Santa Lucia Mountains. Isolated groves are scattered along the southern California coast to San Diego County. Bigleaf maple is common on the western slopes of the Sierra Nevada north of the Yuba River and is present in less abundance as far south as Sequoia National Park *(11)*.

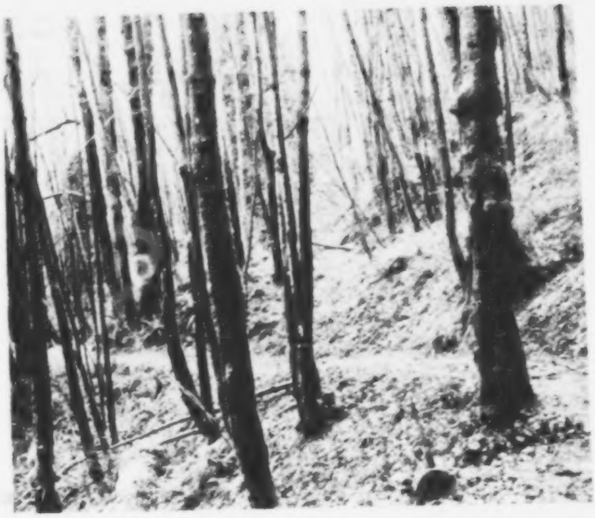

Figure 1—Young bigleaf maples in western Oregon, showing the good form and clean stems typical of dense stands.

Most of the estimated volume of standing sawtimber is found in Washington (about 19.6 million m^3 or 3.43 billion fbm) and Oregon (about 18.0 million m^3 or 3.16 billion fbm). Almost half this timber is in Lewis and Whatcom Counties in Washington and Douglas and Lane Counties in Oregon *(17)*. The estimated 1.1 million m^3 (200 million fbm) of bigleaf maple in British Columbia is found on the south coast and Vancouver Island *(16)*.

Climate

Bigleaf maple grows over a wide range of temperature and moisture conditions, from the cool, moist, marine climate of coastal British Columbia to the warm, dry, growing seasons of southern California (table 1). Springs, streams, and other permanent sources of water are often associated with bigleaf maple in southern California, but it also grows on eastern and northern slopes in California where more than 600 mm (24 in) of annual rainfall occurs *(15)*. It receives abundant moisture in the coastal redwood region of northern California *(36)*. Bigleaf maple is not, however, limited to moist sites in southwestern Oregon, where it is found from moist stream bottoms to dry hillsides. Nocturnal moisture stresses of more than 2.0 M Pa (20 bars) have been recorded on some of those hillsides in southwestern Oregon. This maple also grows on hot, dry sites in the central-western Cascade Range in Oregon and does not seem to be limited by moisture deficiencies there

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Table 1—Climatic variation in northern and southern portions of the native range of bigleaf maple

Areas	Mean temperature			Frost-free period	Mean precipitation	
	Annual	Maximum	Minimum		Annual	Growing season
		°C		*days*	*mm*	
British Columbia[1]	8 to 10	18 to 26	12 to 2	140 to 270	700 to 6600	300 to 1170
California[2]	13 to 15	24 to 27	2 to 6	270 to 350	560 to 1470	50 to 130
		°F		*days*	*in*	
British Columbia	46 to 50	64 to 79	28 to 36	140 to 270	27 to 260	12 to 46
California	55 to 59	75 to 81	36 to 43	270 to 350	22 to 58	2 to 5

[1] Latitudes 49° to 51° N *(20)*.
[2] Latitudes 35° to 37° N *(29)*.

(40). Moisture deficiencies seldom occur in western valleys of the Olympic Peninsula or in coastal British Columbia *(25,32)*. Temperature probably limits the northern distribution of bigleaf maple *(29)*.

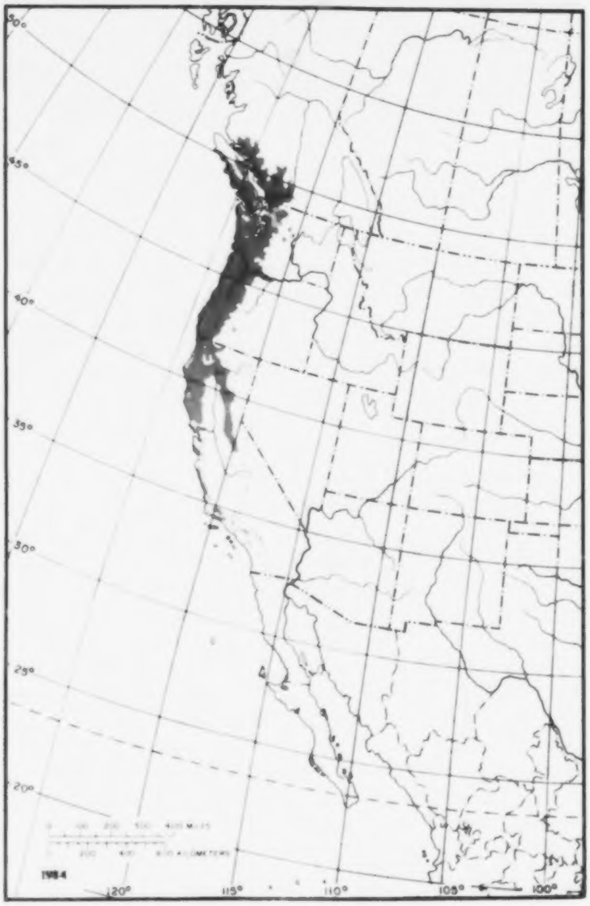

Figure 2—The native range of bigleaf maple.

Soils and Topography

Well drained alluvial and colluvial soils are well suited to bigleaf maple. Abundant moisture and a deep, gravelly profile produce the best growth—usually on river terraces, flood plains, and seepage sites *(25)*. Growth is poorer on shallow, rocky soils, but bigleaf maple is frequently found on such soils. In the Coast Ranges of Oregon and the north Cascade Range in Washington, it even grows on steep talus slopes *(1,5)*.

Bigleaf maple is associated with many soil groups *(5,25)*. On upland sites, these groups include the moist but well drained Brown Soils (Haplumbrepts and Dystrochrepts); Reddish Brown Lateritic soils (Haplohumults); Podzols (Haplorthods); both fine- and coarse-textured dry soils (Haploxerolls and Xeropsamments); and shallow, dry soils (Lithic Xerumbrepts). Soil groups associated with bigleaf maple in lowland areas include flood plain alluvium (Udifluvents); alluvial pumice deposits (Vitrandepts); wet, gley soils (Aqualfs); and cool, acid, well-drained soils (Boralfs). These soil great groups and suborders are found in the soil orders Inceptisols, Ultisols, Spodosols, Mollisols, Entisols, and Alfisols.

Bigleaf maple does not require high concentrations of soil nutrients *(36)*, but it is very sensitive to toxic concentrations of soil boron *(9)*. Litterfall weights are greater under bigleaf maple than under Douglas-fir, and bigleaf maple leaves and litter contain high concentrations of potassium, calcium, and other macro- and micro-nutrients *(6,33)*. Bigleaf maple is a soil-building species that benefits the sites on which it grows.

Bigleaf maples grow at low elevations on the north side of Santa Cruz Island *(27)* but are usually found on riparian sites above 915 m (3,000 ft) in southern California, where the maximum elevation at which they grow is 2135 m (7,000 ft). Farther north in California, maximum elevations decrease to 1675 m (5,500 ft) in the Sierra Nevada and 1035 m (3,400 ft) in the Coast Ranges *(29)*. In central and northern California, bigleaf maple becomes less riparian and more widely distributed *(11)*, sometimes growing as shrubby clumps on the steepest north-facing canyon walls *(15)*. This maple does not grow in the Central Valley of California *(11)*. It is found above 310 m (1,017 ft) in steep-sided ravines and on mesic slopes in the Klamath Mountains *(31)* and at elevations of 1220 m (4,000 ft) on the Cascade Range in southern Oregon.

The topography occupied by bigleaf maple in Oregon and Washington includes flat interior valleys, gently sloping stream bottoms and moderate to steep slopes. It grows on both moist, fertile stream bottoms and arid, precipitous, south-facing rock outcroppings with slopes greater than 100 percent in the Coast Ranges of northwestern Oregon *(1)*. On the Olympic Peninsula in Washington, the maximum elevation at which it grows is 455 m (1,500 ft). Bigleaf maple is seldom found above 305 m (1,000 ft) in coastal British Columbia, but it has been observed above 350 m (1,150 ft) on the east coast of southern Vancouver Island *(25)*.

Associated Forest Cover

Characteristic trees, shrubs, and herbs associated with bigleaf maple in five portions of its native range are listed in table 2. Douglas-fir, Pacific madrone, Pacific dogwood, swordfern, and prince's-pine grow with bigleaf maple in most environments. Bigleaf maple communities often present on moist sites include willow–black cottonwood–bigleaf maple and red alder–bigleaf maple/salmonberry. The bigleaf maple/snowberry *(Symphoricarpos albus)* community is found on dry sites *(5)*. Bigleaf maple is present but is not a dominant species in several other plant communities—western hemlock/western swordfern/Oregon oxalis and Douglas-fir/oceanspray (western Washington and Oregon), Sitka spruce/devilsclub-stink currant *(Ribes bracteosum)* (British Columbia), and white fir/Oregongrape (California), for example.

Bigleaf maple is present in the following forest cover types *(3)*: Red Alder (Society of American Foresters Type 221), Black Cottonwood–Willow (222), Sitka Spruce (223), Western Hemlock–Sitka Spruce (225), Pacific Douglas-Fir (229), Douglas-Fir–Western Hemlock (230), Port-Orford-cedar (231), Redwood (232), Oregon White Oak (233), Douglas-Fir–Tanoak–Pacific Madrone (234), Pacific Ponderosa Pine–Douglas-Fir (244), and Pacific Ponderosa Pine (245).

Bigleaf maple supports several epiphytic plants in moist climates. This support is particularly evident in the "rain forest" on the west side of the Olympic Peninsula, where epiphytes weigh nearly four times as much as the leaves of host bigleaf maples *(19)*. Some of those maples, heavily laden with rain-soaked epiphytes, are more susceptible to windthrow than trees with less luxuriant epiphytic growth *(32)*. A club moss *(Selaginella oregana)* and the mosses *Hylocomium splendens*, *Leucolepis menziesii*, *Isothecium stoloniferum*, and *Neckera menziesii* are the most abundant epiphyte species, but lichens (*Cladonia*, *Nephroma*, and *Crocynia* spp.) and the licorice fern *(Polypodium glycyrrhiza)* are also common *(5,32)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Bigleaf maple begins to produce seed at about 10 years of age and continues every year thereafter *(23)*. It is polygamous, and both staminate and perfect flowers are mixed in the same dense, cylindrical racemes. Flowers are greenish yellow and scented, and they appear before the leaves—from March, at low elevations and in the southern part of the range, to June, at high elevations and in the north. Pollination by insects usually occurs within 2 to 4 weeks after the buds burst *(29)*. Pubescent double samaras result, with 3.5- to 5-cm (1.4- to 2-in) wings that diverge at less than a 90° angle. They ripen in September and October.

Seed Production and Dissemination—Seeds are abundant almost every year, but production by individual trees and stands can vary from year to year *(7)*. Although most of the seeds are dispersed by the wind between October and January, some seeds can be found on trees as late as March. Bigleaf maple seeds are large and generally triangular or oval. They are 4 to 12 mm (0.16 to 0.47 in) long and 4 to 9 mm (0.16 to 0.35 in) thick. At field moisture content, filled-seed weights range from 5,200 to 7,900 seeds/kg (2,400 to 3,600 seeds/lb) for individual trees in the Oregon Coast Range. Seed coat comprises 60 to 70 percent of the seed weight *(39)*.

Seed moisture content reaches a minimum of 10 to 20 percent (dry weight basis) before the autumn rains begin in western Oregon. After the rains begin, seed moisture content varies among individual trees, but it increases by 140 to 200 percent. The pubescent seed coat appears to be effective in holding water and raising seed moisture content quickly. Seed collection and storage are best done when minimum moisture content is reached before the start of the autumn rains. Seeds in this condition can be stored without further drying for at least 1 year at 1° C (34° F) with

Table 2—Characteristic trees, shrubs, and herbs associated with bigleaf maple in five portions of its native range

TREES	SHRUBS	HERBS
SIERRA NEVADA		
White fir (*Abies concolor*) Pacific madrone (*Arbutus menziesii*) Chinkapin (*Castanopsis chrysophylla*) Pacific dogwood (*Cornus nuttallii*) Sugar pine (*Pinus lambertiana*) Ponderosa pine (*Pinus ponderosa*) Douglas-fir (*Pseudotsuga menziesii*) California black oak (*Quercus kelloggii*) Canyon live oak (*Quercus chrysolepis*)	Greenleaf manzanita (*Arctostaphylos patula*) Deerbrush (*Ceanothus integerrimus*) Snowbrush (*Ceanothus velutinus*) Baldhip rose (*Rosa gymnocarpa*)	Trailplant (*Adenocaulon bicolor*) Princes-pine (*Chimaphila umbellata*) Hooker's fairybells (*Disporum hookeri*) Whitevein pyrola (*Pyrola picta*) Pioneer violet (*Viola glabella*)
CALIFORNIA NORTH COAST RANGES		
Pacific madrone Chinkapin Pacific dogwood Tanoak (*Lithocarpus densiflorus*) Ponderosa pine Douglas-fir California black oak Canyon live oak Coast redwood (*Sequoia sempervirens*) California laurel (*Umbellularia californica*)	Blueblossum (*Ceanothus thyrsiflorus*) California hazel (*Corylus cornuta*) Western poison-oak (*Toxicodendron diversilobum*) Box blueberry (*Vaccinium ovatum*) Pacific rhododendron (*Rhododendron macrophyllum*)	Oregon oxalis (*Oxalis oregana*) Western swordfern (*Polystichum munitum*) Bracken (*Pteridium aquilinum*) Whipple vine (*Whipplea modesta*)
KLAMATH MOUNTAINS (SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA)		
White fir Pacific madrone Chinkapin Pacific dogwood Incense-cedar (*Libocedrus decurrens*) Tanoak Ponderosa pine Douglas-fir Canyon live oak Oregon white oak (*Quercus garryana*) California black oak Pacific yew (*Taxus brevifolia*) California laurel	Greenleaf manzanita California hazel Salal (*Gaultheria shallon*) Cascade hollygrape (*Berberis nervosa*) Western poison-oak Baldhip rose California dewberry (*Rubus ursinus*) Oceanspray (*Holodiscus discolor*)	Trailplant Princes-pine Hooker's fairybells Mountain sweetroot (*Osmorhiza chilensis*) Western swordfern Whitevein pyrola Whipple vine
WESTERN WASHINGTON AND OREGON (CASCADE RANGE, COAST RANGES, AND OLYMPIC PENINSULA)		
Grand fir (*Abies grandis*) Vine maple (*Acer circinatum*) Red alder (*Alnus rubra*) Pacific madrone Pacific dogwood Sitka spruce (*Picea sitchensis*) Black cottonwood (*Populus trichocarpa*) Douglas-fir Pacific yew Western redcedar (*Thuja plicata*) Western hemlock (*Tsuga heterophylla*)	Saskatoon serviceberry (*Amelanchier alnifolia*) Cascade hollygrape Salal Box blueberry American devilsclub (*Oplopanax horridum*) Western poison-oak Pacific rhododendron Thimbleberry (*Rubus parviflorus*) Salmonberry (*Rubus spectabilis*) Rustyleaf menziesia (*Menziesia ferruginea*)	Maidenhair fern (*Adiantum pedatum*) Princes-pine Twinflower (*Linnaea borealis*) False lily-of-the-valley (*Maianthemum dilatatum*) Mountain sweetroot Oregon oxalis Western swordfern Ladyfern (*Athyrium filix-femina*)
BRITISH COLUMBIA		
Grand fir Red alder Pacific madrone Pacific dogwood Sitka spruce Black cottonwood Douglas-fir Western redcedar Western hemlock	Saskatoon serviceberry Cascade hollygrape Salal Rustyleaf menziesia Devilsclub Thimbleberry Salmonberry Box blueberry Red huckleberry (*Vaccinium parvifolium*)	Maidenhair fern Western swordfern Deerfern (*Blechnum spicant*) Twinflower False lily-of-the-valley Princes-pine

only a slight loss in viability. Seeds collected after the moisture content has increased are usually killed by redrying, but they can be stored for up to 6 months at the field moisture content with a 30- to 40-percent reduction in viability. Seeds stored in this way produce vigorous seedlings when planted in nursery beds *(39)*.

Seedling Development—Germination is epigeal. It begins in late January or early February under field conditions and is usually completed by April or May in the Oregon Coast Range. Seeds germinate completely at 1° C (34° F) under laboratory conditions, beginning at about 60 days and completing their germination after 90 to 120 days *(39)*. Because of this low temperature threshold for germination, seeds germinate early under natural conditions if moisture is not limiting. Germination during stratification can be used as a means of screening seeds before sowing. If seeds are stratified for 60 days and then germinated, the optimum temperature for germination is 15° C (59° F) *(10)*. Exogenous gibberellin, cytokinin, or ethylene do not overcome the stratification requirement *(10)*. A small number of seeds have been found germinating on trees in December before dispersal *(39)*.

Seed germination is excellent on mineral soil and organic substrates *(7,25,39)*, and seedling establishment is best when those substrates do not dry excessively during the growing season. Bigleaf maple seedling emergence is not affected by Douglas-fir canopy density in coastal Oregon under conditions that vary from young-and-dense to old-and-open stands, but emergence is better under all of these stand conditions than it is in clearcut areas *(7)*. An average 30 to 40 percent of the viable seeds germinate if they are protected from predators, and occasional seed lots attain 80 percent germination *(7)*. All bigleaf maple seeds germinate during the late winter and spring after seed dispersal. Delayed germination does not occur in subsequent years *(7)*.

Bigleaf maple seedlings have a high juvenile growth potential, exceeding that of Douglas-fir and other conifers *(38,39)*. When open-grown under conditions of adequate moisture and nutrients, seedlings reach heights of 1 to 2 m (3.3 to 6.6 ft) in one growing season. Competition affects growth, however, and first-season height is reduced by more than 50 percent when seedling density is increased from 1 to about 600 seedlings/m^2 (0.1 to 55.7 seedlings/ft^2). Seedling weight is even more sensitive to competition than seedling height, and an increase in density from 1 to 60 seedlings/m^2 (0.1 to 5.6 seedlings/ft^2) can result in a 50-percent decrease in seedling dry weight *(39)*.

The morphology of young seedlings is strongly influenced by density. At low density, branch development begins in the buds associated with the cotyledons and moves up the stem as height growth progresses. At high densities, branch development is suppressed and the few branches that develop soon die. Internode length is highly responsive to density, and the longest internodes are produced at intermediate densities during the first year of growth.

The growth potential of bigleaf maple is rarely achieved in the field under normal conditions of light, moisture, competition, and browsing intensity *(7)*. A survey of bigleaf maple seedlings in western Oregon showed that the tallest seedlings were 5 m (16.4 ft) tall and 20 to 30 years old. The height distribution of all seedlings in a stand most commonly resembled an inverted J, with 0 to 25 cm (0 to 10 in) tall, 1- to 4-year-old seedlings, most numerous. Normal and bimodal height distributions were also observed in the western Oregon survey. Although these seedlings were all growing in the understories of Douglas-fir stands, shapes of the height-distribution curves did not seem to be associated with stand conditions. Few seedlings were found in clearcuts *(7)*. Browsing by deer probably is the most important factor influencing the height and stem morphology of bigleaf maple seedlings *(7)*.

Temporary flooding is common on riparian sites, and the seedlings are able to survive short periods of inundation. Bigleaf maple is not as tolerant of flooding as red alder, Oregon ash *(Fraxinus latifolia)*, black cottonwood, Sitka spruce, and western redcedar, however; flooding for 2 months during the growing season kills both maple seedlings and mature trees *(35)*.

Vegetative Reproduction—Bigleaf maple sprouts profusely after being cut. The large stumps produce more and taller sprouts, but all sizes regenerate vigorously. Sprout clumps have achieved heights of 5 m (17 ft) and crown diameters of 6.5 m (21.5 ft) in 3 years, with as many as 67 sprouts around a single stump *(28)*. This sprouting vigor probably could be used in reproducing pure stands of bigleaf maple by the coppice method. It creates undesirable competition for the conifers being managed on most sites. Unlike vine maple *(Acer circinatum)*, bigleaf maple does not appear to reproduce by layering. It can, however, be propagated from stem cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—Rapid height growth of bigleaf maple continues through the sapling stage, but it slows as the trees grow from pole to sawtimber size. Diameter growth is proportional to leaf area, and trees with large crowns develop more sapwood than trees with small crowns *(37)*. The volume of individual trees ranges from 0.11 m^3 (4 ft^3) at 15 cm (6 in) in d.b.h. to 6.5 m^3 (230 ft^3) at 91 cm (36 in) in d.b.h. *(24)*. The largest bigleaf maple known in 1977 grew in western Oregon and had a circumference of 1064 cm (419 in) at breast height, a height of 30.8 m (101 ft), and a crown spread of 27.4 m (90 ft) *(26)*. The oldest attain ages of 200 years or more *(2)*.

Pure, 70-year-old stands of bigleaf maple have yielded about 315 m^3/ha (4,500 ft^3/acre). Under intensive management, rotations of 50 years or less could probably be used *(16)*.

Rooting Habit—Bigleaf maple has a shallow, widespreading root system well suited to the shallow or saturated soils on which it often grows. It probably has a competitive advantage over deeper-rooted species under such conditions.

Reaction to Competition—Bigleaf maple is not a pioneer species that rapidly invades disturbed areas; however, it is often present in undisturbed stands and is able to respond with vigorous sprout growth after disturbance. Maple seedling establishment is most likely to occur in Douglas-fir stands after the start of natural thinning and before the dense understory characteristic of older stands develops. Light or other factors related to stand density apparently limit establishment. Increases in light from 0 to 20 percent of that in the open result in increases of from 0 to 60 percent in survival, but additional increases in light are not beneficial. Seedlings often occur in clusters, with various age distributions, suggesting that conditions favoring establishment vary from year to year *(7)*. The presence of bigleaf maple in undisturbed stands and its potential for rapid growth suggest that it can respond quickly to gap formation or overstory removal.

Maple seedlings often appear in intermediate or late seral communities. Bigleaf maple frequently follows willow *(Salix* spp.) or red alder in riparian seres *(4,13)*, and sometimes it replaces oaks or Pacific madrone on upland sites.

Silviculture of bigleaf maple usually involves control rather than culture. Bigleaf maple does not aggressively invade clearcut units, but vigorous stump sprouting is a problem when it occurs in the harvested stand. Sprouting can be controlled by applying water-soluble amines or potassium salts of phenoxy herbicides around the sapwood perimeter on freshly cut stumps *(21)*. Girdling the uncut trees is ineffective, for girdled bigleaf maples survive for several years and sprout. Aerial spraying of herbicides and other foliar applications are also ineffective—herbicide translocation is inadequate and the roots are not killed *(22)*. Basal bark treatments overcome this problem. They are effective when ester-in-oil formulations of the phenoxy herbicides are applied *(21)*.

Dry sites with bigleaf maple overstories should not be clearcut if conversion to Douglas-fir is attempted. Seedling survival will be better if the Douglas-fir is underplanted, preferably after the overstory maples are killed with a basal spray of phenoxy ester in oil *(20)*.

When bigleaf maple is harvested as a crop rather than killed as a weed, often only trees that will yield a minimum log size (3.7 m by 25 cm, or 12 ft by 10 in) are harvested *(16)*. Merchantable trees are usually scattered, limbing is laborious, and logs are short. Felling, yarding, and milling costs therefore tend to be higher for bigleaf maple than for conifers. Mill waste is also high—as much as 30 percent in slabs, sawdust, trim, and defect *(16)*.

Damaging Agents—Fungi are responsible for much of the defect in bigleaf maple. Decay is seldom a serious problem in young undamaged trees, but stem and branch wounds are invaded by wood-rotting fungi such as *Heterobasidion annosum*, *Fomitopsis pinicola*, *Polyporus berkeleyi*, and *Inonotus dryadeus* that can reduce the tree to a hollow shell. Overmature bigleaf maples are often decayed by root rot *(Armillaria* spp.) and butt rots *(Ganoderma applanatum* and *Oxyporus populinus)*. Verticillium wilt *(Verticillium albo-atrum)* occasionally kills forest trees, but it is most serious on ornamental bigleaf maples *(14)*.

The carpenter worm *(Prionoxystus robiniae)* may seriously damage living maples. It attacks trees of all sizes, particularly those that are open grown. The resulting larval tunnels degrade the lumber cut from affected stems. Dead trees and maple products are damaged by powderpost beetles *(Hemicoelus*, *Melalgus*, *Polycaon*, *Ptilinus*, *Scobicia*, and *Xestobium* spp.), and a roundheaded borer *(Synaphaeta guexi)* makes large burrows in dead or dying trees *(8)*.

Bigleaf maple twigs and young stems are browsed by deer and elk. They are also clipped by mountain beavers. The roots are sometimes attacked by nematodes *(Meloidogyne* spp.) *(14)*. A high percentage of seedling mortality also results from predation by rodents and grazing by slugs and other invertebrates *(7)*.

Seed predation by small mammals is high, and it may be related to overstory condition. Seedling emergence on artificially seeded plots in the Oregon Coast Range is from 7 to 100 times greater on plots protected from birds and rodents than on unprotected plots. The highest rate of predation is in young (20- to 40-year-old) and old (80- to 250-year-old) stands with lower rates in clearcuts and in pole-size stands (40 to 80 years old) *(7)*.

Special Uses

Bigleaf maple is an excellent shade tree. Its wood is used in the furniture industry, but it is neither as hard nor as strong as the wood of sugar maple *(Acer saccharum) (16)*. Like sugar maple, it has sweet sap that can be made into syrup. The flow of sap is adequate for syrup production in January and February, but the syrup is of a lower quality than that made from sugar maple *(30)*.

Bigleaf maple is a preferred wood for piano frames. It is excellent for decorative face veneer and makes good container material but is not suitable for flooring *(16)*. The amounts of bigleaf maple being marketed for fuelwood are increasing as the use of wood stoves increases. Bigleaf maple has about 70 percent of the fuel value of Oregon white oak and 115 percent of the fuel value of red alder wood.

Bigleaf maple is usually harvested in conifer stands along with the conifers. These trees generally originate from sprouts and are of poor quality. Higher quality trees could be produced by managing maple stands that originate from seed or planted seedlings.

Genetics

The Kimball maple *(Acer macrophyllum* Pursh var. *kimballi* Harrar), a rare variety of bigleaf maple, occurs in the Washington counties of Snohomish, Cowlitz, and Pierce. It differs from *Acer macrophyllum* var. *macrophyllum* in having much more deeply lobed leaves, often tricarpellate flowers, and frequent triple samaras *(12)*.

Acer macrophyullum Pursh forma *rubrum* Murray is an even rarer form of bigleaf maple. First noticed at Berkeley, CA, in 1968 and later found in the Coast Ranges north of San Francisco, it has red leaves *(18)*. The young leaves of an early German cultivar, 'tricolor,' are also red. Tricolor leaves are rose-red, however, and they later become marked with white.

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Acer negundo L. Boxelder

Aceraceae Maple family

Ronald P. Overton

Boxelder (*Acer negundo*) is one of the most widespread and best known of the maples. Its other common names include ashleaf maple, boxelder maple, Manitoba maple, California boxelder, and western boxelder. Best development of the species is in the bottom-land hardwood stands in the lower Ohio and Mississippi River valleys, although it is of limited commercial importance there. Its greatest value may be in shelterbelt and street plantings in the Great Plains and the West, where it is used because of its drought and cold tolerance.

Habitat

Native Range

Boxelder (figs. 1, 2) is the most widely distributed of all the North American maples, ranging from coast to coast and from Canada to Guatemala. In the United States, it is found from New York to central Florida; west to southern Texas; and northwest through the Plains region to eastern Alberta, central Saskatchewan and Manitoba; and east in southern Ontario. Further west, it is found along watercourses in the middle and southern Rocky Mountains and the Colorado Plateau. In California, boxelder grows in the Central Valley along the Sacramento and San Joaquin Rivers, in the interior valleys of the Coast Range, and on the western slopes of the San Bernardino Mountains. In Mexico and Guatemala, a variety is found in the mountains. Boxelder has been naturalized in New England, southern Quebec, New Brunswick, Nova Scotia, and Prince Edward Island; and in the Pacific Northwest in southeastern Washington and eastern Oregon.

Climate

Boxelder's wide range shows that it grows under a variety of climatic conditions. Its northward limits are in the extremely cold areas of the United States and Canada, and planted specimens have been reported as far north as Fort Simpson in the Canadian Northwest Territories (*2*). Although boxelder is most commonly found on moist soil, it is drought tolerant and is frequently used in windbreaks and around homesteads throughout the Plains (*21*). It has also been known to survive inundation for as long as 30 days (*15*).

Soils and Topography

Boxelder has been found on virtually all types of soils, from heavy clays to pure sands of the orders Entisols, Inceptisols, Alfisols, Ultisols, and Mollisols. It is most common on deep alluvial soils near streams, but it also appears on upland sites and occasionally on poor, dry sites (*11,13*). Through most of its range it grows in areas of little topographic relief, except for those features associated with stream valleys. In southern and central Arizona and New Mexico the species is found up to 2440 m (8,000 ft) (*23*) and in Mexico up to 2680 m (8,800 ft) (*18*), but even at these elevations it is confined to stream bottoms and wet draws.

Associated Forest Cover

Boxelder is most commonly found in association with bottomland hardwoods. It is an associate species in the following cover types (Society of American Foresters) (*8*):

Eastern	
42	Bur Oak
61	River Birch–Sycamore
62	Silver Maple–American Elm
63	Cottonwood
87	Sweetgum–Yellow-poplar
93	Sugarberry–American Elm–Green Ash
94	Sycamore–Sweetgum–American Elm
95	Black Willow
109	Hawthorn
Western	
235	Cottonwood–Willow
236	Bur Oak

Other associates in the eastern United States include red maple (*Acer rubrum*), hackberry (*Celtis occidentalis*), slippery elm (*Ulmus rubra*), black walnut (*Juglans nigra*), basswood (*Tilia americana*), black cherry (*Prunus serotina*), blackgum (*Nyssa sylvatica*), pecan (*Carya illinoensis*), Nuttall, water, willow, and overcup oak (*Quercus nuttallii*, *Q. nigra*, *Q. phellos*, and *Q. lyrata*), persimmon (*Diospyros virginiana*), and baldcypress (*Taxodium distichum*). In the Plains region, boxelder appears with green ash (*Fraxinus pennsylvanica*), bur oak (*Quercus macrocarpa*),

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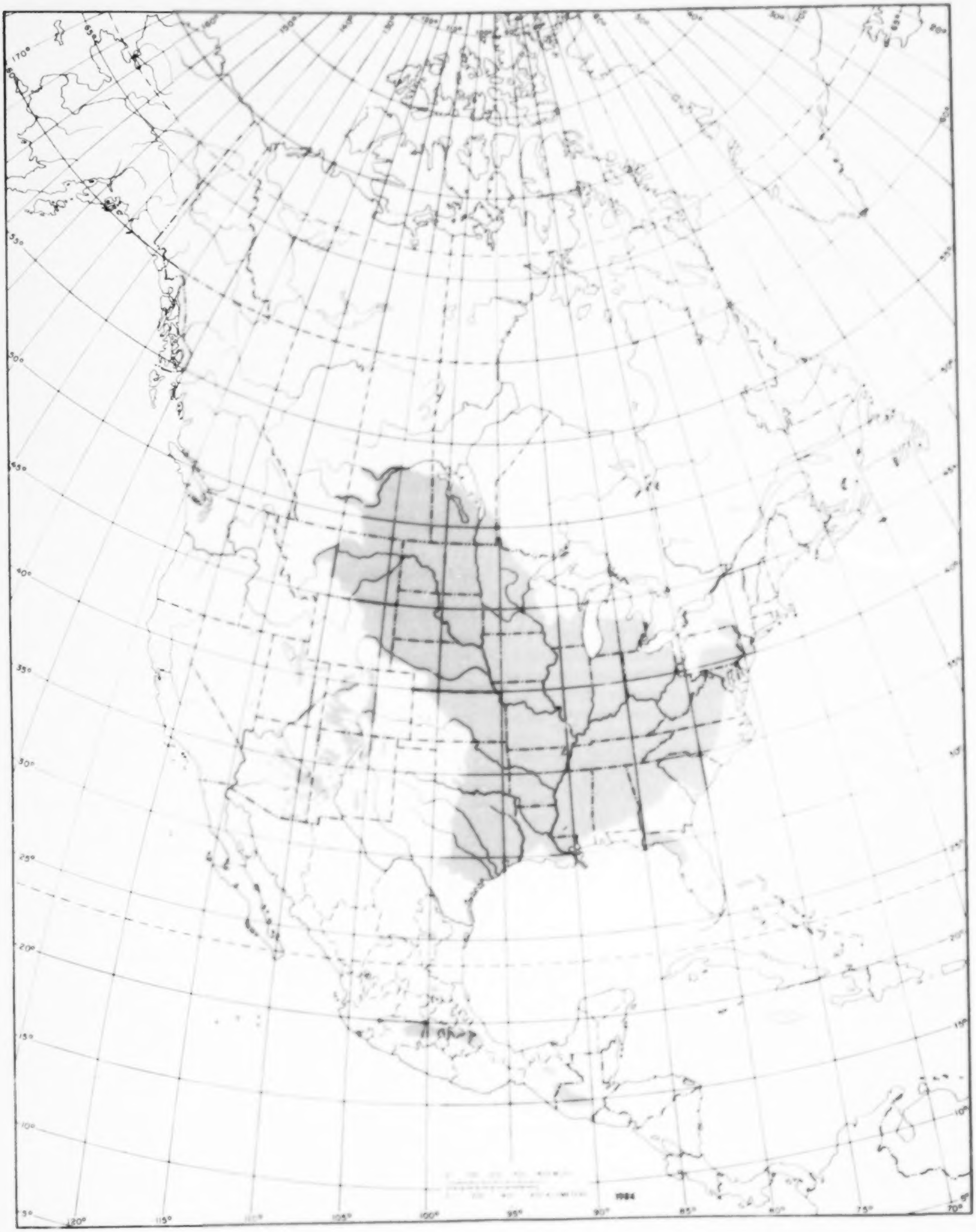
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Figure 1—*The native range of boxelder.*

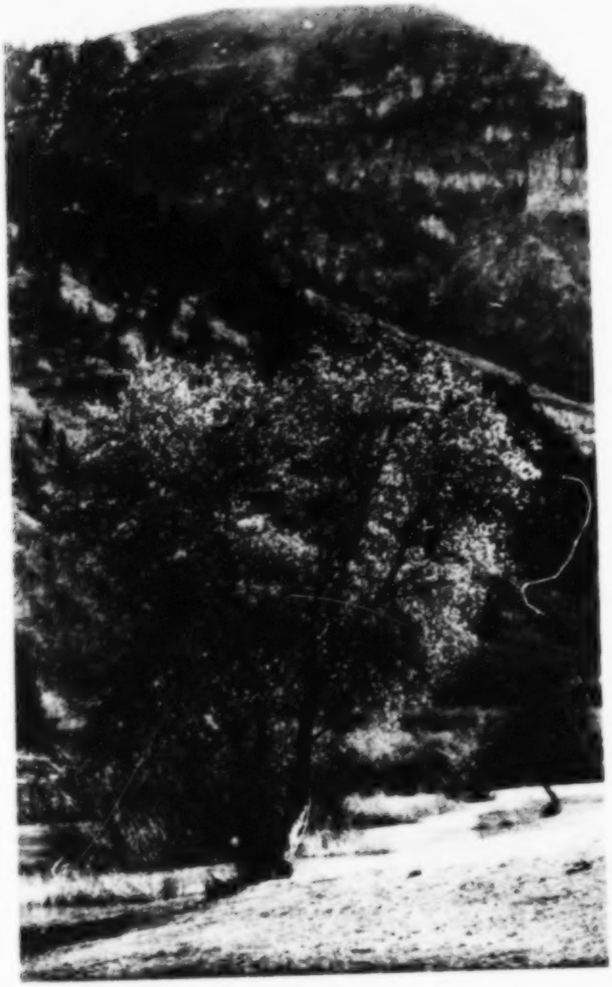

Figure 2—*Boxelder.*

plains cottonwood (*Populus deltoides* var. *occidentalis*), willow (*Salix* spp.), and hackberry. In the Rocky Mountains and the Colorado Plateau, associates include several species of willow and cottonwood, netleaf hackberry (*Celtis reticulata*), and Arizona sycamore (*Platanus wrightii*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Boxelder is dioecious with imperfect flowers, although perfect flowers that appeared to be functional have been reported (*12*). The staminate flowers are fascicled, the pistillate flowers are drooping racemes and are wind pollinated (*21,23*). Flowers appear with or before the leaves from March to May, depending on the geographic location (*13,28*).

Seed Production and Dissemination—Seed crops are produced each year on individual boxelder trees beginning at 8 to 11 years of age. The samaras are borne on drooping racemes and average 29 500/kg (13,400/lb) (*26*). Ripening takes place from August to October and seeds are wind distributed continuously until spring. This extended period provides a variety of germination sites, moisture, and temperature combinations and may account for the prolific reproduction from seed that is common for the species (*11*).

Seedling Development—Boxelder is capable of establishing itself on a variety of seedbeds. On southern Illinois bottom lands, it is among the most abundant species seeding in under cottonwood-willow and "soft" hardwood stands and invading old fields. On these sites, overstory density is apparently not a factor in early germination and survival, but seedlings begin to die off after 1 or 2 years unless openings are provided. The 1- and 2-year-old boxelder seedlings are also abundant in areas of ground vegetation ranging from light to heavy and in hardwood litter as much as 5 cm (2 in) deep (*16*).

Methods of collecting, handling, storing, and testing boxelder seeds have been described (*3,4,26*). Germination is epigeal.

Vegetative Reproduction—Reproduction by stump and root sprouts is common in boxelder from young, vigorous trees (*8,18*). Reports on propagation by cuttings indicate that best results are obtained from cuttings taken during the period of transition from softwood to greenwood and treated with an 8,000 ppm IBA-talc mixture (*7*). European nurserymen propagate some ornamental cultivars of boxelder using side grafts, whip and tongue grafts, or chip budding (*7*).

Sapling and Pole Stages to Maturity

Growth and Yield—Boxelder is a small to medium-size tree reaching 15 to 23 m (50 to 75 ft) in height and 60 to 120 cm (24 to 48 in) in d.b.h. The species is short-lived, attaining an average age of 60 years but rarely 100 years. Growth during the first 15 to 20 years is very rapid and may be as much as 2.5 cm (1 in) a year in d.b.h. (*11*). Poor sites bring a corresponding reduction in growth. In western Minnesota windbreaks, diameter growth averaged less than 5 mm (0.2 in) per year and height growth averaged less than 0.37 m (1.2 ft) per year during the first 13 years after planting *(25)*. Boxelder typically forms a short, tapering bole and bushy, spreading crown.

Because boxelder usually appears in mixed stands and has limited commercial value, no information is available about its potential yield. Equations are available, however, to predict volume of boxelder stems, and green and dry weights of stems, limbs, and leaves *(24)*. After trees reach 15 cm (5.9 in) in d.b.h., the proportion of aboveground green components is relatively constant, with bole wood, 63 percent; bole bark, 8 percent; limbs, 22 percent; and leaves, 7 percent.

Rooting Habit—Boxelder usually develops a shallow, fibrous root system. On deep soils it may form a short taproot with strong laterals *(11)*.

Reaction to Competition—In the area of its best development, the lower Ohio and Mississippi River valleys, boxelder usually follows the pioneer species of cottonwood and willow in colonizing new ground in alluvial bottoms. In some instances it is a pioneer species in the invasion of old fields *(16)*. Boxelder may persist into the oak-hickory type but then begins to be eliminated, probably due to shading *(18)*. The species is generally classed as tolerant of shade, although less so than the other soft maples *(13)*.

Damaging Agents—The chief rot-causing fungi attacking boxelder are *Fomitopsis fraxinus, Perrenniporia fraxinophilus, Fomes geotropus, Fomitopsis scutellata, Inonotus glomeratus,* and *Ustulina vulgaris.* Root rots caused by *Rhizoctonia crocorum* and *Phymatotrichum omnivorum* have been identified on boxelder, but *Armillaria mellea* has not been reported on the species, although it is common on other maples *(14)*.

Verticillium wilt *(Verticillium albo-atrum)* is the only notable killing disease of boxelder. The species is also susceptible to a stem canker caused by *Eutypella parasitica.*

A red stain in the wood of living trees caused by *Fusarium reticulatum* var. *negundinis* apparently is specific to boxelder. The stain regularly is associated with Cerambycid beetles and the galleries of other insects, but itself does no damage to the wood *(14)*.

Insect damage to boxelder is relatively unimportant, but a number of leaf-feeding and scale insects and borers attack it *(1)*. The boxelder bug, *Leptocoris trivittatus* is a common associate of boxelder throughout most of its range. The nymphs feed mainly on pistillate trees in leaves, fruits, and soft seeds. Although the trees are not greatly damaged, the insect's habits of invading houses in large numbers with the onset of cold weather makes it an important pest. The boxelder aphid, *Periphyllus negundinis,* and the boxelder gall midge, *Contarinia negundifolia,* are also common. Other leaf feeders include the Asiatic garden beetle, *Maladera castanea,* the greenstriped mapleworm, *Anisota rubicunda,* a leafroller, *Archips negundana,* and the boxelder leafroller, *Caloptilia negundella.* The scale insects include cottony maple scale, *Pulvinaria innumerabilis,* and terrapin scale, *Mesolecanium nigrofasciatum.* Borers include the boxelder twig borer, *Proteoteras willingana,* and the flatheaded apple tree borer, *Chrysobothris femorata.*

Ice and wind damage is common in older trees *(11)* and boxelder is quite susceptible to fire and mechanical damage due to its thin bark.

Boxelder is highly sensitive to 2,4-D. In the northern Great Plains, drift from agricultural spraying operations produced distorted, blighted foliage up to 16 km (10 mi) from the source *(20)*.

Special Uses

Because of its drought and cold resistance, boxelder has been widely planted in the Great Plains and at lower elevations in the West as a street tree and in windbreaks. Although the species is not an ideal ornamental, being "trashy," poorly formed, and short-lived, numerous ornamental cultivars of boxelder are propagated in Europe *(7)*. Its fibrous root system and prolific seeding habit have led to its use in erosion control in some parts of the world *(32)*.

Seeds and other portions of boxelder are utilized by many species of birds and mammals as food *(19)*. Because of the species delayed seeding habit, some seeds are available throughout most of the winter. The sap of boxelder has been used to a limited extent for syrup *(9)*.

Genetics

Population differences in boxelder have been noted in response to photoperiod *(6,28)*, in seed germination and stratification requirements *(29)*, seed weight *(30)*, tracheid length *(31)*, frost tolerance *(5)*, and in chlorophyll levels *(10)*.

Some 8 to 14 varieties and forms have been described for boxelder, several relating to variegated patterns of the foliage or some other morphological character *(2,17,21,23,28)*. At least two varieties appear to be confined to a definite geographic range:

var. *arizonicum* Sarg. to central and southern Arizona and New Mexico and var. *californicum* (Torr. and Gray) Sarg. to the Central Valley, Coast Range, and San Bernardino Mountains of California *(23)*.

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Acer nigrum Michx. f. **Black Maple**

Aceraceae Maple family

William J. Gabriel

Black maple *(Acer nigrum)*, also called black sugar maple, hard maple, or rock maple, is closely related to sugar maple *(A. saccharum)* in habit, range, and quality and use of wood. Black maple grows on a variety of soils, but most commonly on moist soils of river bottoms in mixed hardwood forests. It grows rapidly in early life, then slowly and may live 200 years. Black maple is cut and sold with sugar maple as hard maple lumber. The trees can be tapped for sap for making maple syrup. Young trees are often browsed by deer, and buds and seeds are eaten by birds. Occasionally this tree is used as an ornamental.

Habitat

Native Range

Black maple (fig. 1) extends from New England, New York, and southern Quebec west through southern Ontario to central Michigan, northern Wisconsin, and southeastern Minnesota; south to northeastern Kansas and Missouri; and east in Tennessee to western North Carolina, Virginia, West Virginia, Maryland, Pennsylvania, and New Jersey. It was once found in Delaware but is now extinct there *(20)*.

Black maple increases in frequency from east to west. It is the only form in the sugar maple complex found in central and western Iowa, where it appears to be better adapted to the warmer and drier prairie climate. At the onset of these conditions, sugar maple begins to drop out, but black maple continues westward some 193 km (120 mi) beyond the western limits of sugar maple *(1)*.

Black maple is found with sugar maple over a large part of its range (fig. 2). In the cooler, more moist eastern section, sugar maple is better adapted to the climate and introgression into black maple occurs. Black maple, considered a relict of an earlier exerothermic climatic era, is only sparsely represented in the area *(8)*.

Climate

The important climatic factors within the range of black maple are as follows: normal annual total precipitation, 610 to 1420 mm (24 to 56 in); growing season precipitation, 300 to 510 mm (12 to 20 in); average annual snowfall, 15 to 150 cm (6 to 60 in) *(28)*; average annual minimum temperature -12° to -34° C (10° to -30° F); average length of frost-free period, 120 to 210 days; precipitation effectiveness index (effectiveness of precipitation at the temperature at which it fell), 48 to 127 *(19,29)*.

The factors limiting the distribution of black maple are a combination of temperature and moisture. A comparison of its range with that of closely related sugar maple shows that sugar maple extends about 4 degrees in latitude farther into the cooler north and ranges northeast into the mainland provinces of Canada, well into lower Quebec. But to the west, black maple extends into the warmer, drier, subhumid grasslands 193 km (120 mi) farther than sugar maple, whose distribution ends at the western boundary of the humid forest zone. The importance of temperature and precipitation effectiveness is further reflected in only scattered appearances of black maple in predominantly sugar maple stands in Quebec, where they are considered relicts of a past warm, dry period *(8)*.

Soils and Topography

Several general soil types lie within the range of black maple. In the cooler, more moist areas they are podzolic (order Spodosols), subject to mineral and organic losses through leaching and eluviation. In the warmer and more temperate sections are melanized, cryptorganic, and vadose soils of sialic substrata. In the drier, subhumid western areas of its range, the invasion of the prairies by forests has resulted in degraded chernozems or embryonic groods *(30)*. These soils are included in the orders Mollisols, Inceptisols, Entisols, and Spodosols.

In the part of the black maple range included in northwestern Ohio, northern Indiana, and southwestern Michigan, the soils are light in color and low in organic matter; there are dark-colored, poorly drained areas dispersed among them. These soils were developed from various types of glacial deposit and are variable in texture *(23)*.

In western Ohio, black maple increases in abundance as the soil type changes from a silty clay loam to a silt loam, indicating that poorer aeration and internal drainage react unfavorably with the taxon *(26)*.

In central Iowa, black maple is found on well-drained, moderate slopes with dark topsoils 20 to 25

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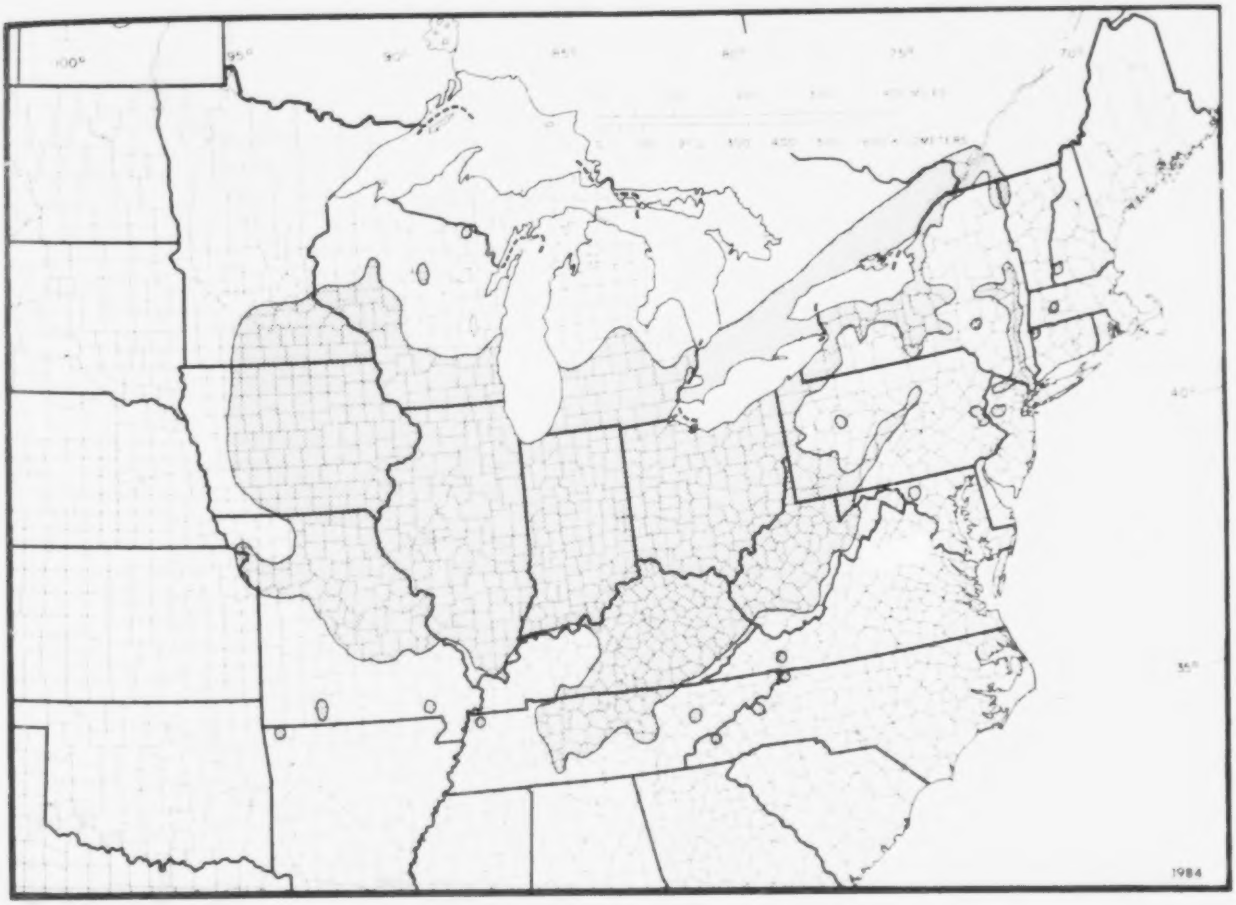

Figure 1—*The native range of black maple.*

cm (8 to 10 in) deep, grading into a subsoil that is yellow-brown clay, changing to calcareous clay till at 75 cm (30 in) *(18)*.

In Quebec and New York, black maples are restricted to rich, low grounds with a limestone substratum *(11)*. In central and northern Missouri, black maple in association with other species is found in rich woods, on slopes, in ravines and valleys, and near streams *(27)*.

In a study of black maple originating in glaciated and unglaciated areas of Ohio, it was concluded that the present-day population is a postglacial hybrid swarm between black and sugar maple, and that black maple had not been subjected to strong selection forces as the result of glaciation *(22)*.

Associated Forest Cover

Black maple has been treated taxonomically as a species or as a subspecies in the sugar maple complex *(20,25)*. In most practical forest treatments, because of its similarities in wood properties, black maple has been included with sugar maple and treated as a subspecies. Although their ranges overlap and black maple appears with sugar maple in a number of forest types, black maple is not usually listed as a component of these types. In some areas, black maple is found in large numbers; in others, sugar maple is found in nearly pure stands.

Oak-hickory and maple-beech-birch are major forest types in which black maple is an associate *(19)*.

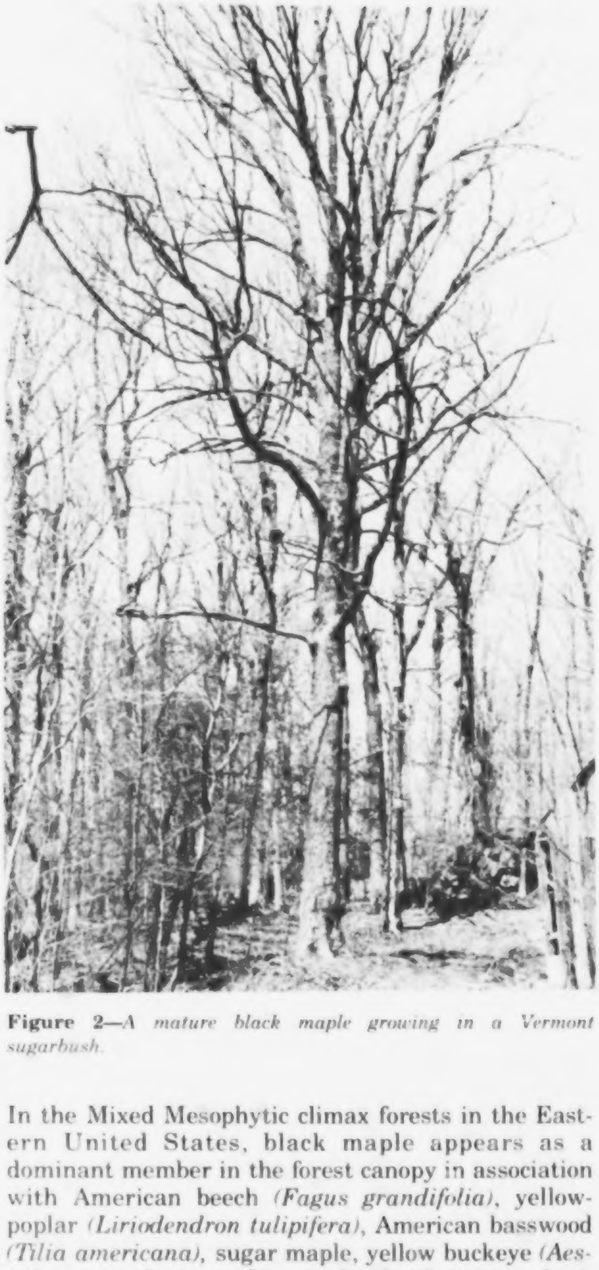

Figure 2—*A mature black maple growing in a Vermont sugarbush.*

In the Mixed Mesophytic climax forests in the Eastern United States, black maple appears as a dominant member in the forest canopy in association with American beech *(Fagus grandifolia)*, yellow-poplar *(Liriodendron tulipifera)*, American basswood *(Tilia americana)*, sugar maple, yellow buckeye *(Aesculus octandra)*, northern red oak *(Quercus rubra)*, white oak *(Q. alba)*, and eastern hemlock *(Tsuga canadensis) (5)*.

The black maple-basswood association on north slopes in central Iowa represents a transition from a beech-maple climax centered in Ohio *(18)*. On flood plains, the principal species in a transitional community are American basswood, slippery elm *(Ulmus rubra)*, American elm *(U. americana)*, and black maple *(5)*. In five forest stands that were predominantly black maple, the proportion of commercially important species was as follows: black maple, 30.8 percent; American basswood, 14.9 percent; northern red oak, 8.5 percent; American elm, 7 percent; black walnut *(Juglans nigra)*, 5 percent; white ash *(Fraxinus americana)*, 3.5 percent; slippery elm, 3.5 percent; white oak, 3 percent; bitternut hickory *(Carya cordiformis)*, 2.5 percent; eastern redcedar *(Juniperus virginiana)*, 1.5 percent; bur oak *(Quercus macrocarpa)*, 0.5 percent; shagbark hickory *(Carya ovata)*, 0 to 5 percent (unpublished data, North Central Forest Experiment Station, St. Paul, MN).

In central Kentucky, on the lower slopes of ravines, black maple is well represented in mixture with American beech, white ash, blue ash *(Fraxinus quadrangulata)*, yellow-poplar, white oak, northern red oak, and chinkapin oak *(Quercus muehlenbergii) (5)*.

The understory vegetation associated with black maple is quite variable because of the variation in habitat over its range. On melanized loam soils in the Lake States area, the shrub understory consists mainly of Atlantic leatherwood *(Dirca palustris)* and species of *Viburnum*, blackberries and raspberries *(Rubus)*, and elder *(Sambucus)*. Ground cover commonly found in the area includes maidenhair fern *(Adiantum pedatum)*, sweet jarvil *(Osmorhiza claytonii)*, red baneberry *(Actaea rubra)*, early meadowrue *(Thalictrum dioicum)*, Dutchmans-breeches *(Dicentra cucullaria)*, rue anemone *(Anemonella thalictroides)*, wild sarsaparilla *(Aralia nudicaulis)*, and bristly greenbrier *(Smilax hispidia) (30)*.

In the unglaciated highland area of southern Indiana, where black maple is well represented, as many as 40 species have been listed in the herbaceous layer of the forest *(5)*. Some of the most prominent plants in the understory are the common pawpaw *(Asimina triloba)*, spicebush *(Lindera benzoin)*, poison-ivy *(Toxicodendron radicans)*, and horsebrier *(Smilax rotundifolia) (24)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The yellowish-green flowers of black maple are borne on pendulous, hairy pedicels that are 3 to 7 cm (1.2 to 2.8 in) long, in subsessile corymblike inflorescences. Female flowers are found mainly in terminal buds; lateral buds usually contain male flowers with few or no female flowers.

Like sugar maple, black maple is monoecious. Flowers are pseudohermaphroditic (flowers may be morphologically perfect but functionally they are unisexual) and occur in mixed buds. The rachis of the inflorescence results from the differentiation of the vegetative shoot. The latter is laid down first in the bud and consists of two pairs of leaves and a short stem. The leaves are arranged in an upright, protective manner about the lower part of the inflorescence. There is little difference in external morphology between vegetative and flower-containing buds when in deep dormancy.

The first expression of a break in dormancy is the swelling of the mixed buds, which take on a four-sided appearance. After budburst, the inflorescence develops more rapidly than the leaves. The time for full development of flowers depends on the air temperature but normally occurs in 3 to 4 days. Duration of stigma receptivity may range from 3 days during warm, dry periods to 8 days during cool, moist periods.

The same dichogamous condition found in sugar maple is found in black maple. Protandry, or a male-female sequence in flower blooming, occurs in some trees while protogyny, or a female-male sequence, occurs in others *(13)*. Pollination of female flowers is by wind and bees.

In Vermont, the average flowering period is the first week in May. May is the average month for flowering in Indiana and Michigan *(10)*, but over its entire range, April is considered the average month for flower blooming *(25)*.

Fruits that contain seeds are treated for germination as for sugar maple *(7)*. After a 24-hour initial soaking in water, the seeds are stratified in a moist media. Germination is epigeal and starts with the appearance of a radicle about 6 weeks after stratification. Within a week to 10 days, a pair of cotyledons appears, followed by a pair of primary leaves. Two pairs of secondary leaves replace the primary leaves and a terminal bud is set, provided soil moisture is adequate. Second, and occasionally third, flushes of growth may occur during the growing season.

Seed Production and Dissemination—Black maple fruits are paired samaras, fused at the pericarps and each with a papery wing ranging in length from 15 to 30 mm (0.6 to 1.2 in) and in width from 5 to 15 mm (0.2 to 0.6 in). Wings may be divergent or parallel in varying degrees. At seedfall, the fruits split apart and the peduncles remain on the tree. Fruit and seed size vary from tree to tree. Smaller fruits and seeds appear to be related to more divergent wings. Within trees, fruits and seeds are relatively uniform.

In ripening fruits, the pericarp changes from green to brownish or reddish green. The outer integument of the seed changes from silver to brown. The seeds are exalbuminous, having no endosperm. Fruits of black maple ripen on schedule in the fall with sugar maple fruits. In New England, seedfall occurs in late September and early October, depending on latitude and altitude. Heavy seed crops usually occur in 4-year cycles in Vermont and surrounding States, with lighter seed production during intervening years. Although the fruits and seeds are moderately heavy, during high winds the papery wing of the fruits can carry the seed considerable distances from the seed tree. Size and weight of black maple fruits and seeds follow closely those of sugar maple, which averages 15.500 seeds per kilogram (7,030/lb) *(28)*.

Seedling Development—Black maple produces a sufficient quantity of seeds and subsequent seedlings to reproduce itself over its entire range but finds more optimum conditions for reproduction in the midwestern and western parts of its range. In a maple-basswood community located on a north slope in central Iowa, one seedling count was 40,150/ha (16,250/acre). On a western slope dominated by oaks and hickories, the count dropped to 8,400/ha (3,400/acre), and under floodplain conditions, 740/ha (300/acre) *(1)*. Germination of black maple seeds is epigeal *(26)*. In central Kentucky, black and sugar maple together with beech are successfully reproduced on limestone soils on lower slopes. On the upper slopes, a great increase in the abundance of black maple in the understory indicates a movement of black maple and other species from the lower to the upper slopes at the expense of oaks and hickories *(5)*.

The scattered growth of black maple in cooler, more moist southern Quebec and northern New England indicates it cannot compete successfully with sugar maple in these areas *(9,11)*. The few stands in southern Quebec where black maple still can be found are considered remnants of an earlier warmer and drier period *(9)*.

Survival and growth of outplanted black maple seedlings in experimental plantings are similar to that of sugar maple (fig. 3). Seedlings of both taxa during the initial developmental stages in the plantation require protection from competing vegetation and gnawing rodents. Where deer are prevalent, protection must be provided or seedlings should be planted that are tall enough to extend beyond their reach.

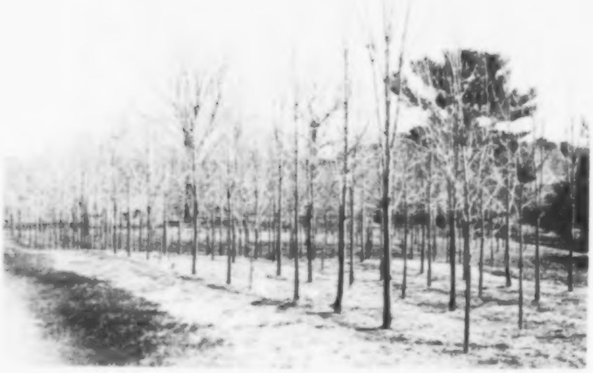

Figure 3—*A young mixed plantation of control-pollinated black and sugar maples and hybrids growing in Vermont.*

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—The average height and diameter of black maple after six growing seasons in a transplant bed were 1.9 m (6.3 ft) and 21 mm (0.84 in), respectively. Among plantation-grown black maple (fig. 3), the average height and d.b.h. after nine growing seasons were 4.9 m (16.1 ft) and 6.4 cm (2.5 in), respectively. Mature trees reach heights of 21 to 34 m (70 to 110 ft) and more than 100 cm (40 in) in d.b.h. *(4)*.

In central Iowa, the average height of maple trees ranged from 14 to 23 m (43 to 75 ft). The median diameter class was 20 cm (8 in) in d.b.h. Black maples in maple-basswood communities were adversely affected when subjected to a severe drought *(1)*. Total volume of all commercially important species in five stands dominated by black maple was 191 m^3 (6,756 ft^3), of which 73 m^3 (2,564 ft^3) or 39 percent was black maple (unpublished data, North Central Forest Experiment Station, St. Paul, MN).

Rooting Habit—No information available.

Reaction to Competition—Black maple is classed as very tolerant of shade. Seedlings prosper under heavy forest cover and trees respond to release even after extreme and prolonged suppression.

Damaging Agents—The damaging agents of black maple are considered to be the same as those for sugar maple.

Special Uses

The wood properties of black and sugar maple overlap in a narrow range and for all practical purposes are considered the same. A sampling of black maple trees showed that the average vessel segment length was 340 μ; the average fiber length was 845 μ. Sugar maple had 15 percent more uniseriate rays than black maple *(21)*.

Black maples are tapped for sap in the process of making maple syrup. Tests on unreplicated plots of black and sugar maple showed little differences between the two taxa in the sugar content of sap *(16)*.

In Marshall County, IN, individual volume tables were developed for both black and sugar maple. These were combined when statistical analysis indicated no significant differences *(15)*.

Genetics

There appear to be two broad populations of black maple with respect to its hybridizing with sugar maple. One is in the western part of its range, where it maintains its identity and shows little tendency to cross with sugar maple *(2,3,12,27)*. The second population is in the eastern section, where it hybridizes readily with sugar maple *(9,11)*. Evidence of this has, in most cases, been based on studies of leaf characters, which are considered more useful in systematic studies than other characters such as flowers, fruits, and winter buds *(12)*.

In speculating on the hybrid origin of black maple, one of the parents advanced is sugar maple. On the basis of an "average" leaf constructed from numerous leaves of maple that were collected over its range, it has been hypothesized that the second parent is Rugel maple (*Acer saccharum* var. *rugelii* (Pax) Rehder) *(6,25)*. The foliar stipules at the base of leaf petioles of black maples (fig. 4) are not found on either proposed parents and may represent a reversion resulting from gene interaction in the hybrid.

In the Northeast, black and sugar maple are separate populations with distinct characters that are united by a large intermediate population which includes a variety of recombinations from the two taxa. Introgression by sugar maple occurs because of differences in ecological requirements. The cooler, more moist climate favors the survival of those hybrids and back-cross progenies that tend to be more like sugar maple than black maple *(9)*.

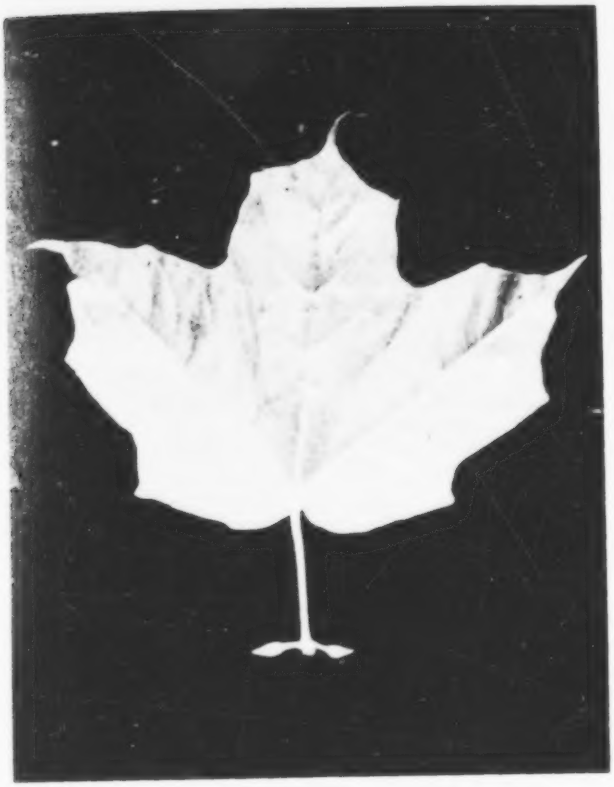

Figure 4—*Foliar stipules at the base of a black maple leaf stem.*

Systematic studies have been based mainly on observations of herbarium specimens of leaves collected over the range of black and sugar maple. Hybridization has been verified through intermediacy of leaf characters, but controlled pollinations have been successful between the two taxa using parents of Vermont origin *(14)*. Crosses using sugar maple as a female parent were more successful than those using black maple as a female. Hybrid leaf shapes favored sugar maple in outline, but pubescence was intermediate. With a little practice, workers could easily distinguish hybrids between the two taxa among mixed 5-year-old stock—representing both straight sugar maple and black maple progenies and hybrids—by the intermediate pubescence and by differences in leaf lobules.

In a provenance study of sugar maples, which included some black maples, height growth of the latter ceased earlier, fall foliage color developed sooner, and leaf fall occurred earlier than that of sugar maple *(17)*. Exceptions were black maples from Iowa, which showed no differences from sugar maple. Young black maple trees showed less forking, or a higher degree of apical dominance, than sugar maples of the same age.

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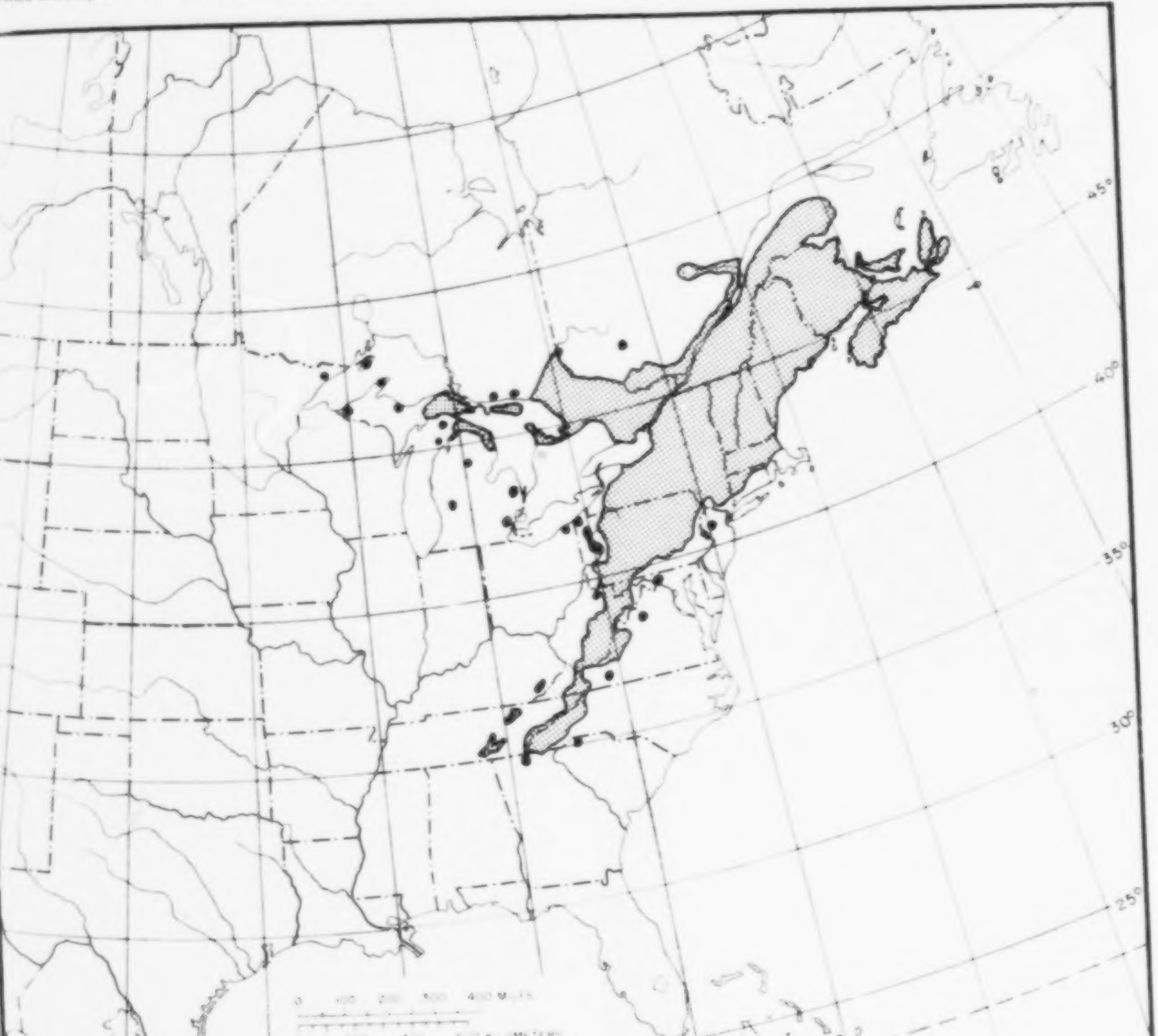
Acer pensylvanicum L. Striped Maple

Aceraceae Maple family

William J. Gabriel and Russell S. Walters

Striped maple (*Acer pensylvanicum*) (8), also called moosewood, is a small tree or large shrub identified by its conspicuous vertical white stripes on greenish-brown bark. It grows best on shaded, cool northern


45°
40°
35°
30°
25°
20°
100°
90°
80°
70°
0 100 200 300 400 MILES
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1984

Figure 1—*The native range of striped maple.*

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slopes of upland valleys where it is common on well-drained sandy loams in small forest openings or as an understory tree in mixed hardwoods. This very slow growing maple may live to be 100 and is probably most important as a browse plant for wildlife, although the tree is sometimes planted as an ornamental in heavily shaded areas *(33,37)*.

Habitat

Native Range

Striped maple (figs. 1, 2) is widely distributed over the northeastern quarter of the United States and southeastern Canada. Its natural range extends from Nova Scotia and the Gaspé Peninsula of Quebec, west to southern Ontario, Michigan, and eastern Minnesota; south to northeastern Ohio, Pennsylvania, and New Jersey, and in the mountains to northern Georgia *(28)*. The species is distinct from other maples, and there is no evidence of intergrading with other species.

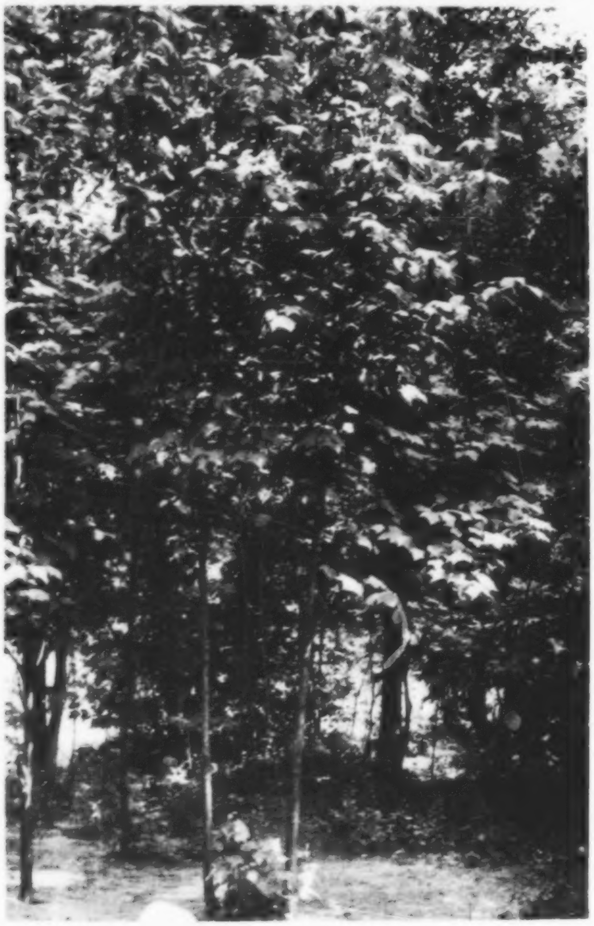

Figure 2—*Striped maple.*

Climate

The important climatic factors within the range of striped maple are as follows: total annual precipitation, 710 to 1630 mm (28 to 64 in); normal monthly growing season precipitation (May, June, July, and August), 50 to 100 mm (2 to 4 in) in the northern and eastern part of the range and from 100 to 200 mm (4 to 8 in) in the central and southern sections; mean annual total snowfall, 5 to 250 cm (2 to 100 in) with pockets up to 500 cm (200 in); mean length of frost-free period between the last 0° C (32° F) temperature in the spring and the first 0° C (32° F) in the autumn, 90 to 210 days; and average January temperature, -12° C (10° F) to 4° C (40° F) *(43)*.

Soils and Topography

Striped maple is found on brown and gray-brown podzolic soils (orders Inceptisols, Alfisols, and Spodosols) that characterize the areas of mixed coniferous and hardwood forests. It also grows on the strongly weathered and leached podzols (order Spodosols) as well as on darker melanized soils (order Mollisols) *(3,47)*. Compared to other species in the genus *Acer*, which are relatively indifferent to soil reaction, striped maple prefers acid soils *(42,45)*. Neither the range in soil pH nor the optimum acidity level is known for the species.

Soil moisture and texture influence the local distribution of striped maple. It is common on sandy loams that are moist and well drained *(23,42)*. A study of local distribution in western Massachusetts showed that on study plots where striped maple was present there was a positive correlation between species density and windthrow mounds that resulted in small openings in the stand. No significant correlations were found with depths of organic and A horizons, rock outcrops, or stoniness of soils *(13,16)*.

In areas of granitic drift in the White Mountains of New Hampshire, striped maple of sapling size was most abundant (15 percent of total basal area) on soils with a matrix of sharp-angled or rounded boulders or on nearly pure weathered granite found not more than 65 cm (26 in) below the top of mineral soil *(24)*. On wet compact till and on washed till, the species made up 6.8 percent and 7.3 percent of the stand basal area, respectively. It is one of five species that seems to be permanent and abundant in local distribution on a well-drained, fine, sandy loam podzol in the White Mountains *(23)*.

Striped maple and its associates are found on glaciated knoll tops and slopes in Quebec *(26)*. In the mountainous areas of New England, it develops best at elevations between 550 and 800 m (1,800 and 2,600 ft) *(2,42)*. It apparently does not do well at higher elevations in the northeast. In two transects beginning at 610 and 630 m (2,000 and 2,070 ft) at different locations in the White Mountains of New Hampshire, striped maple was only 2 to 4 percent of the basal area of the forest stand *(25)*. It dropped out completely between elevations of 830 and 860 m (2,720 and 2,820 ft).

Density of striped maple in western Massachusetts increased with a slope up to 45° and with an elevation up to 700 m (2,300 ft) *(13,16)*. Growth increased on northerly facing, local aspects and on steeper slopes and towards the top of slopes. In the southern Appalachian Mountains, the species is common on mesic sites with an elevation between 760 and 1370 m (2,500 and 4,500 ft); above this elevation it disappears very rapidly *(46)*.

Striped maple attains its best growth on shaded, cool northern slopes in deep valleys *(18)*. It can exist under a number of different combinations of environmental factors, but as a mesophyte it favors habitats where moisture conditions are moderate.

Associated Forest Cover

Striped maple is a common but minor forest component, appearing as an understory species in the boreal hardwoods and in the spruce-fir and northern hardwood types of the northern forest region. It is a part of the undergrowth vegetation in 12 of the following eastern forest cover types (Society of American Foresters) *(7)*.

17	Pin Cherry
20	White Pine–Northern Red Oak–Red Maple
22	White Pine–Hemlock
23	Eastern Hemlock
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
28	Black Cherry–Maple
30	Red Spruce–Yellow Birch
31	Red Spruce–Sugar Maple–Beech
32	Red Spruce
35	Paper Birch–Red Spruce–Balsam Fir
60	Beech–Sugar Maple

In the boreal hardwoods, striped maple is found in association with the following overstory species: pin cherry (*Prunus pensylvanica*), quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), paper birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), balsam fir (*Abies balsamea*), and red spruce (*Picea rubens*).

In the spruce-fir cover types in the northern forest region, the dominant species in association with striped maple are red spruce, gray birch (*Betula populifolia*), American mountain ash (*Sorbus americana*), American beech, and sugar maple. In the northern hardwoods, the most common overstory species are sugar maple, American beech, yellow birch, black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*) *(2,13,16,42)*. Striped maple in the southern Appalachian Mountains appears with eastern hemlock, Carolina silverbell (*Halesia carolinc*), yellow buckeye (*Aesculus octandra*), sugar maple, white basswood (*Tilia heterophylla*), yellowwood (*Cladrastis kentukea*), black birch (*Betula lenta*), and witch-hazel (*Hamamelis virginiana*) *(46)*.

The most common understory species associated with striped maple in addition to reproduction of the overstory species are hobblebush (*Viburnum alnifolium*), Canada yew (*Taxus canadensis*), mountain maple (*Acer spicatum*), woodsorrell (*Oxalis* spp.), eastern hophornbeam (*Ostrya virginiana*), American hornbeam (*Carpinus caroliniana*), serviceberry (*Amelanchier* spp.), hawthorn (*Crataegus* spp.), and pawpaw (*Asimina triloba*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sex expression in striped maple is variable. It can be monoecious, with male and female flowers on the same tree, or dioecious, with some trees male and others female *(11,18,33,35,38)*; the same tree may differ in expression from year to year *(13,21)*.

Sex expression varied in a sample of 312 trees taken under natural habitat conditions in western Massachusetts. Four percent of the trees sampled were monoecious and 96 percent were dioecious. The ratio of female to male flowering trees under the latter condition was 8 to 1 *(15)*.

Sex expression changed for six of eight specimens of striped maple growing under arboretum conditions in Europe. In annual observations made over a period of 2 to 6 years, dioecy appeared 15 times and monoecy 10 times *(21)*. The ratio of male to female trees under the dioecious conditions was 1 to 14.

There is a strong possibility that sex expression is influenced by environmental effects. In one year, 27 trees of 243 changed sex. Most changes were from male to female *(13,15)*. Trees bearing female flowers tended to be less vigorous than those bearing male flowers. Flowering trees, including both sexes, averaged 52/ha (21/acre). As an understory tree, striped maple has a high mortality rate. During the year, nearly 65 percent of the female trees under observation died.

Striped maple produces a crop of flowers each year, under either arboretum *(21)* or natural *(13,15)* conditions. Blooming occurs in May and June *(40)* and begins after the leaves are nearly mature *(1,35,38)*. Flowers are usually pseudohermaphroditic, yellow, and about 6 mm (0.25 in) in diameter, occurring in pendulous racemes that range from 10 to 15 cm (4 to 6 in) in length.

Functional male flowers have a rudimentary pistil that may occasionally be absent; functional female flowers develop stamens but the pollen sacs do not dehisce. A few flowers have been found that appear to be functionally perfect. Flowering may occur among trees as young as 11 years old and as small as 1 m (3.3 ft) in height *(13,15)*.

Fruits of striped maple are samaras borne on pedicels ranging from 10 to 15 mm (0.4 to 0.6 in) in length. Their color is somewhat reddish in early development, changing later to tan. Wings are widely divergent with nutlets about 20 mm (0.8 in) long.

Seed Production and Dissemination—Most fruits and seeds of striped maple ripen in September and October and are dispersed in October and November *(40)*. Seed production varies from tree to tree; some trees produce as few as 10 seeds, whereas others produce several thousand. The density of seed dispersal from a tree drops quickly as the distance from the tree increases. At 10 m (33 ft) from a seed tree the average number of seeds was 13.75 per square meter (1.28/ft^2). At 60 m (200 ft) the number dropped to 1.25 seeds per square meter (0.1/ft^2). Seeds that fall on crusted snow cover may be blown as far as 4 km (2.48 mi) from the seed tree *(14)*. The number of cleaned seeds varies from 21,400 to 34,400/kg (9,700 to 15,600/lb) averaging 24,500/kg (11,100/lb) *(40)*.

Seedling Development—Newly collected striped maple seeds are dormant and must receive moist stratification at 5° C (41° F) for 90 to 120 days to germinate *(40)*. Mature seeds covered only by the current year's leaf litter do not germinate until the second year but, if buried under soil or humus, germinate the first year. There also seems to be a testa-imposed dormancy in the species which causes mechanical restriction of radicle elongation. Seeds would not germinate after stratification of 30 to 90 days with the testae intact, but when testae were removed from over the radicles, germination was rapid and complete. Unstratified seeds with the testae removed from over the radicles and treated with benzyladenine germinated 100 percent at 23° C (74 F) *(49)*.

Delay in germination of striped maple seed was reduced when two-thirds of the basal area of the stand was removed and was completely eliminated when the stand was clearcut *(29)*. In the clearcut, however, total germination dropped sharply with the complete removal of the overstory.

Seed germination is epigeal, with the radicle first to emerge. Soon after the emergence and elongation of the radicle, the shoot begins its upward growth. The cotyledons unfold and are followed by the formation of the first pair of leaves. The leaf margins are serrate and lobes are usually absent. The leaf area is small, ranging from about 25 to 65 mm (1 to 2.5 in) *(5)*.

Suppressed new seedlings generally grow less than 30 mm (1.2 in) per year and mortality is nearly 90 percent after the first growing season. In the following 15 years, the mortality rate drops to less than 1 percent per year. Between 15 and 40 years of age, mortality rises to 3.8 percent per year but drops to 1.6 percent after 40 years *(13,14)*.

Vegetative Reproduction—Vegetative reproduction does not seem to play an important part in the reproduction of the species. Although striped maple reproduces by layering and basal sprouting, sampling of a striped maple population showed that only 3 percent of the trees originated from layering and 8 percent by sprouting *(15)*. In general, natural vegetative propagation of the species seems to be a mechanism by which it survives suppression rather than increasing its numbers. The first leaves of sprouts are small, with coarse serrations, and are unlobed. Sprouting begins relatively soon after a tree dies. Sprouts appeared around the main stem of understory trees within 2 months after main stems were killed in a prescribed burn.

In vitro culture of striped maple has been successful. Callus tissue was formed in a medium consisting of a mixture of coconut milk, naphthalene acetic acid, sucrose, and salt *(31)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Striped maple develops best under moderate light intensity. Rapid shoot growth under low light intensity can occur but the growth resembles etiolation *(48)*. Under direct sunlight striped maple may be succeeded by mountain maple *(19)*.

The species is well adapted to survival under heavy shade. As a suppressed understory tree, its growth and development are extremely slow. Height growth over a 10-year period may be as little as 30 cm (12 in), but trees that have been heavily suppressed for 35 to 40 years respond well to release *(13,14)*.

Growth rate of trees following the removal of the overstory is correlated with growth rate before overstory removal, whether or not they were previously growing in a suppressed or released state. The maximum rate of growth observed among released striped maple under optimum light was 1 m (3.3 ft) per year. The species grows well in small forest openings and under a thinned overstory that results in moderate understory lighting. Because its maximum height growth is about 15 m (49 ft), it will never become a major member in the upper canopy of the northern hardwood forest cover type, though the species has been known to occupy forest openings for more than 100 years *(13,14)*.

Rooting Habit—The root system of striped maple is shallow and wide-spreading *(18)*, illustrating its adaptation to an understory position in the forest. Because it is protected from wind damage by the dominant trees in the overstory, it does not need a deep root system designed for strong support, and its shallow, spreading features make it strongly competitive for soil moisture and nutrients.

Reaction to Competition—The species is ideally suited to expanding and developing its understory position in the forest should the situation arise. Large numbers of small trees that are capable of surviving from year to year under heavy shade await a disturbance in the upper canopy. They show an instant response to increased light even though overtopped for as long as 35 to 40 years. The species does not require full sunlight to realize its maximum growth potential but grows best under moderate lighting found in partial or small forest openings. Striped maple is classed as very tolerant of shade. Sexual reproduction in striped maple is closely associated with changes in the upper canopy, resulting in regeneration of the trees that will be stored in the understory *(13,15)*. Asexual propagation is capable of regenerating individual trees within a few months.

Striped maple is often considered a serious silvicultural problem. When large numbers of this species occupy an understory before cutting, they frequently become the dominant vegetation after cutting, excluding more desirable species *(17)*. In Allegheny hardwood stands in northwestern Pennsylvania, Marquis and others *(30)* found that when more than 30 percent of the 1.83-m (6-ft) radius regeneration plots had more than eight striped maple seedlings before clearcutting, these species became dominant after cutting. If the number of striped maple stems exceeds these recommendations, it is essential to reduce their number before harvest cutting to permit establishment of regeneration of desirable hardwood species. Striped maple can be controlled with glyphosate applied with a mistblower at the rate of 1.12 kg/ha (1 lb/acre) a.i. Best kill was achieved when applied from July 1 through September 1 *(17)*.

Damaging Agents—Probably the most serious enemy of striped maple is Verticillium wilt (*Verticillium albo-atrum*), a soil-borne stem disease that kills the trees it attacks *(12)*. Less destructive to the species is *Cristulariella depraedens*, one of the common leaf spot diseases found on a number of other maple species *(36)*. Although Pezicula trunk and branch cankers are found on several maple species, *Pezicula subcarnea* attacks striped maple only *(9)*. *P. acericola* occasionally appears on striped maple but is most common on mountain maple.

The species is relatively free of insect attack. However, it is subject to infestation by one of the flatheaded borers, *Agrilus politus*, which forms stem galls *(4)*.

Special Uses

Probably the most important use of striped maple is for wildlife food. It is one of the preferred species for rabbits and is frequently eaten by porcupines *(6,34)*. It provides browse for deer and moose, though the net energy derived from winter browse is relatively low *(27,32,44)*. The samaras are eaten, to a limited extent, by ruffed grouse *(22)*. When *Populus* species are lacking, striped maple is eaten by beavers and it is browsed by woodland caribou during summer months *(41,44)*.

Striped maple is occasionally planted as an ornamental tree. Because it does poorly in full sunlight, it must be planted with other species. It was introduced into England about 1760, and into continental Europe shortly thereafter where reportedly it reached heights of 9 to 12 m (30 to 40 ft) with trunk diameters up to 45 cm (18 in).

The wood of the species is diffuse-porous, white, and fine grained, and on occasions has been used by cabinet makers for inlay material. Botanists who visited North America in the early 18th century found that farmers in the American colonies and in Canada fed both dried and green leaves of the species to their cattle during the winter. When the buds began to swell in the spring, they turned their horses and cows into the woods to browse on the young shoots.

An active antitumor substance has been isolated from striped maple, and tests are underway to determine its practical application *(10)*.

Genetics

No organized genetics research has been conducted in striped maple, probably because of its lack of commercial value. The species hybridizes in nature with Tatarian maple *(Acer tatarium)* as the female parent, resulting in the hybrid *A. boscii (20)*. Striped maple has a chromosome complement of n=13, determined from specimens collected from several northern localities. No marked meiotic irregularities were observed. The species appears to be diploid over the northern part of its range *(38)*.

Sex expression was studied in two different samples of 69 and 243 trees each in western Massachusetts. Results of both samples were nearly identical, implying that no genetic differences existed in sex expression between the two areas sampled and that samples came from the same population with respect to the character sampled.

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Acer rubrum L. Red Maple

Aceraceae Maple family

Russell S. Walters and Harry W. Yawney

Red maple *(Acer rubrum)* is also known as scarlet maple, swamp maple, soft maple, Carolina red maple, Drummond red maple, and water maple *(33)*. Many foresters consider the tree inferior and un-

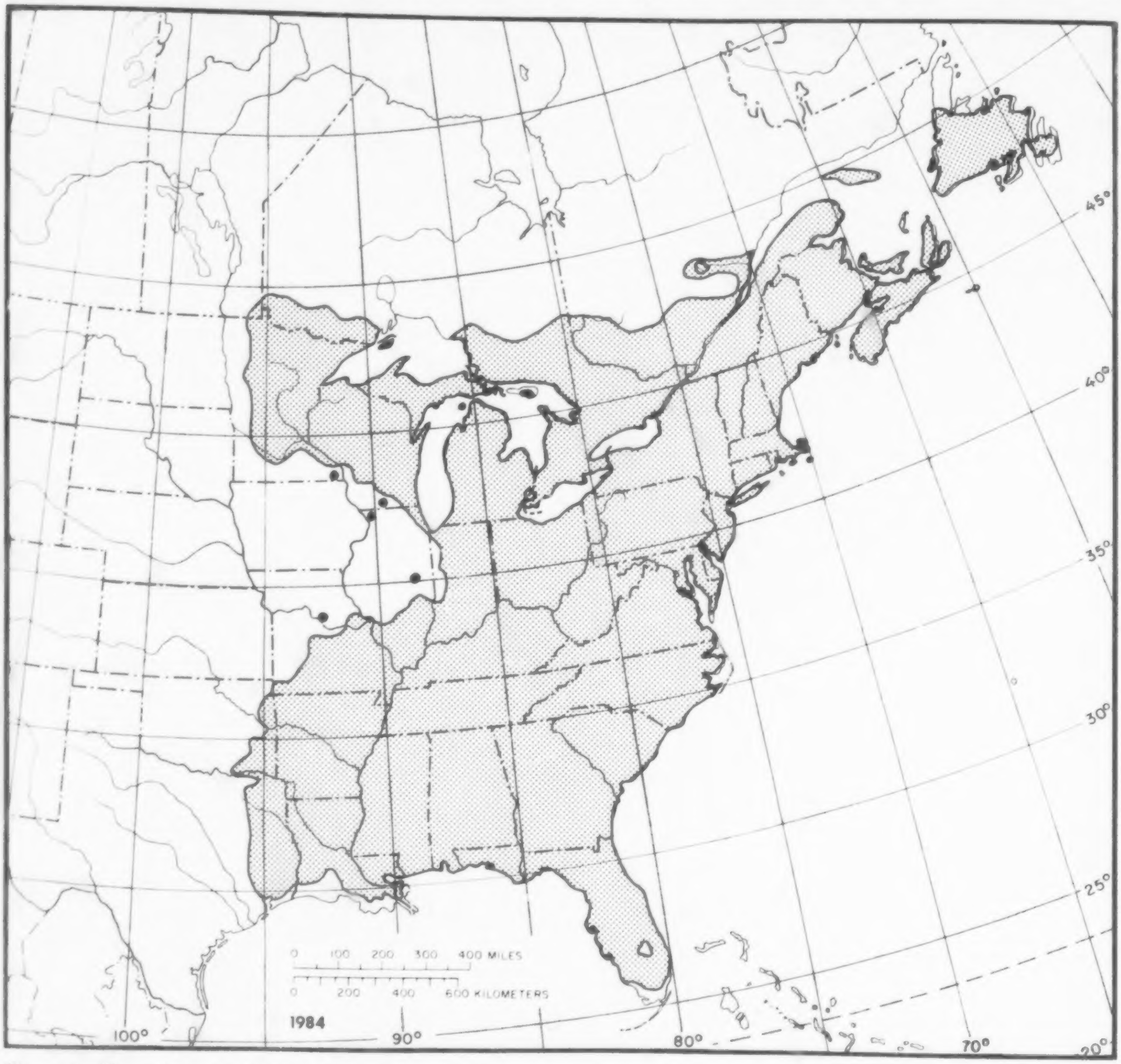
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
1984
100°
90°
80°
70°
45°
40°
35°
30°
25°
20°

Figure 1—*The native range of red maple.*

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desirable because it is often poorly formed and defective, especially on poor sites. On good sites, however, it may grow fast with good form and quality for saw logs. Red maple is a subclimax species that can occupy overstory space but is usually replaced by other species. It is classed as shade tolerant and as a prolific sprouter. It has great ecological amplitude from sea level to about 900 m (3,000 ft) and grows over a wide range of microhabitat sites. It ranks high as a shade tree for landscapes.

Habitat

Native Range

Red maple (figs. 1, 2) is one of the most abundant and widespread trees in eastern North America *(26)*. It grows from southern Newfoundland, Nova Scotia, and southern Quebec to southern and southwestern Ontario, extreme southeastern Manitoba, and northern Minnesota; south to Wisconsin, Illinois, Missouri, eastern Oklahoma, and eastern Texas; and east to Florida *(33)*. It has the greatest continuous range along the Atlantic Coast of any tree found in Florida—an extent of 2575 km (1,600 mi) *(32)*. The species is native to all regions of the United States east of the 95th meridian, with three exceptions: Prairie Peninsula proper of the Midwest, the coastal prairie of southern Louisiana and southeastern Texas, and the swamp prairie of the Florida Everglades. The most notable exception is the Prairie Peninsula, where red maple is absent from the bottom land forests of the Corn Belt, though it grows abundantly in similar situations and species associations both to the north and south of the Peninsula *(54)*.

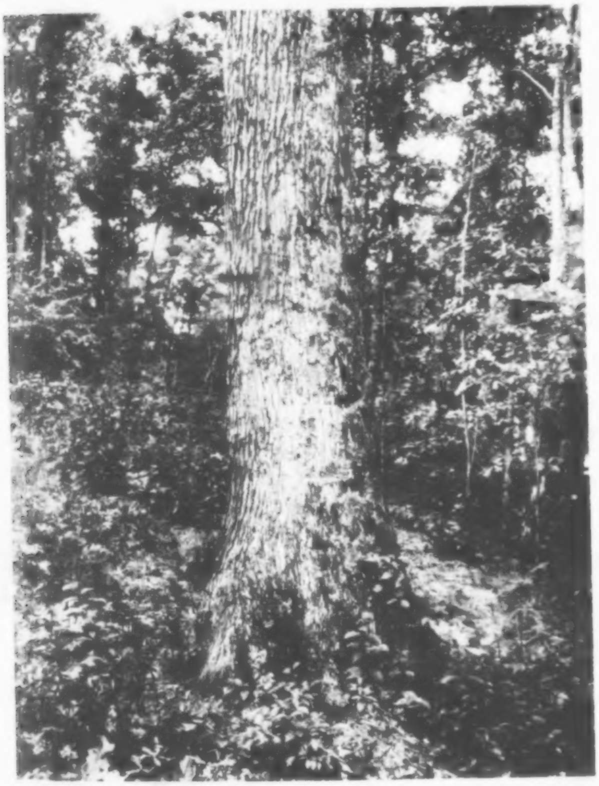

Figure 2—*Mature red maple.*

Climate

The northern extent of the red maple range coincides with the –40° C (–40° F) mean minimum isotherm in southeastern Canada *(11)*. The western range is limited by the dry climate of the Prairie States. Of all the maples, it has the widest tolerance to climatic conditions. The absence of red maple in the Prairie Peninsula does not seem to be related to precipitation amount because the tree grows elsewhere with similar or less annual precipitation.

Soils and Topography

Red maple can probably thrive on a wider range of soil types, textures, moisture, pH, and elevation than any other forest species in North America *(18)*. Its range covers soils of the following orders: Entisols, Inceptisols, Ultisols, Alfisols, Spodosols, and Histosols. It grows on both glaciated and nonglaciated soils derived from granite, gneisses, schists, sandstone, shales, slates, conglomerates, quartzites, and limestone *(26)*.

Red maple grows on diverse sites, from dry ridges and southwest slopes to peat bogs and swamps. It commonly grows under the more extreme soil-moisture conditions—either very wet or quite dry. The species does not show a strong affinity for either a north or a south aspect *(48)*. Although it develops best on moderately well-drained, moist sites at low to intermediate elevations, it is common in mountainous country on the drier ridges and on south and west exposures of upper slopes. It is also common, however, in swampy areas, on slow-draining flats and depressions, and along small sluggish streams *(26)*. In upper Michigan and New England, red maple grows on ridge tops and dry sandy or rocky upland soils and in almost pure stands on moist soils and swamp borders *(13,40)*. In the extreme south, red maple is almost exclusively a swamp species.

Associated Forest Cover

Red maple is a major or an associated species in 56 of the 88 nontropical forest cover types recognized for the eastern United States *(13)*. Red maple forms a pure cover type (Society of American Foresters Type 108) because it makes up at least 80 percent of the stand basal area. The species is also at least 20 percent of Gray Birch–Red Maple (Type 19), White Pine–Northern Red Oak–Red Maple (Type 20), Black Cherry–Maple (Type 28), and Black Ash–American Elm–Red Maple (Type 39).

The red maple is most common in New England, Middle Atlantic States, upper Michigan, and northeast Wisconsin. It is rare farther west and south. Recognition of red maple as a separate cover type generally is attributed to disturbances that allowed red maple residuals to respond rapidly. The elimination of elm *(Ulmus americana* and *U. thomasii)* by Dutch elm disease and of the American chestnut *(Castanea dentata)* by the blight, and selective removal of yellow birch *(Betula alleghaniensis)* and sugar maple *(Acer saccharum)* have contributed to increasing the proportion of red maple stocking in many stands *(13,40,48)*.

Throughout its range, red maple is associated with more than 70 different commercial tree species *(26)*. Its more common associates from the north to the south include red spruce *(Picea rubens)*, balsam fir *(Abies balsamea)*, white pine *(Pinus strobus)*, sugar maple, beech *(Fagus grandifolia)*, yellow birch, paper birch *(Betula papyrifera)*, gray birch *(B. populifolia)*, sweet birch *(B. lenta)*, eastern hemlock *(Tsuga canadensis)*, eastern hophornbeam *(Ostrya virginiana)*, striped maple *(Acer pensylvanicum)*, northern white-cedar *(Thuja occidentalis)*, aspen *(Populus grandidentata* and *P. tremuloides)*, black ash *(Fraxinus nigra)*, pin cherry *(Prunus pensylvanica)*, black cherry *(P. serotina)*, northern red oak *(Quercus rubra)*, American elm, chestnut oak *(Q. prinus)*, Virginia pine *(Pinus virginiana)*, yellow-poplar *(Liriodendron tulipifera)*, silver maple *(Acer saccharinum)*, black gum *(Nyssa sylvatica)*, swamp white oak *(Quercus bicolor)*, and loblolly pine *(Pinus taeda)* *(13)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red maple is one of the first trees to flower in the spring, generally several weeks before vegetative bud break. The flowers are small, with slender stalks, red or rarely yellowish, with petals; they appear from March to May depending upon elevation and latitude. Trees can flower and bear seed at an early age; 4-year-old trees have produced seed. Flowering occurs on all branches in the well-lit upper portion of the crown. Characteristically, the nonflowering branches are slow growing and lack vigor.

Red maple flowers are structurally perfect. The species is polygamo-dioecious. Thus, some trees are entirely male, producing no seeds; some are entirely female; and some are monoecious, bearing both male and female flowers. On monoecious trees, functioning male and female flowers usually are separated on different branches. Sex of the flower is not a function of tree vigor. The species shows a tendency toward dioeciousness rather than toward dichogamy *(59,64,67)*.

Seed Production and Dissemination—A seed crop occurs almost every year, and on an average, a good to bumper crop occurs once in every 2 years *(14)*. Red maple is generally very fruitful. Trees 5 to 20 cm in d.b.h. (2 to 8 in) can yield seed crops of 12,000 to 91,000 seeds. A 30-cm (12-in) tree yielded nearly a million seeds *(1)*. It is possible to stimulate red maple seed production through fertilization. The stimulation often lasts 2 years and may yield up to 10 times more seeds than an unfertilized stand *(4)*.

The fruit, a double samara, ripens from April to June before leaf development is complete. After ripening, seeds are dispersed for a 1- to 2-week period during April through July. The seed does not require pregermination treatment and can germinate immediately after ripening. The fruits are among the lightest of the maple fruits, averaging about 51,000 cleaned seeds per kilogram (23,000/lb). In general, fruits are heavier in northern latitudes. Red maple fruit from Canada, Wisconsin, and Michigan, where the normal growing season is 80 to 150 days, averaged 23 gr (1.5 g)/100 fruits. On the other hand, in Rhode Island, Kentucky, and South Carolina, with a frost-free period of 180 to 240 days, the weight averaged 17 gr (1.1 g)/100 fruits. Because the fruits are small and winged, they disperse efficiently in the wind. Germination may be 75 to 80 percent in 2 to 6 days. Total germination is often 85 to 91 percent *(59,66)*.

Seedling Development—Red maple has few germination requirements. The seed can germinate with very little light *(26)*, given proper temperature and some moisture. Most seeds generally germinate in the early summer soon after dispersal. Shading by a dense overstory canopy can depress first-year germination; then second-year germination is common *(36)*. Germination is epigeal *(59)*.

Moist mineral soil seems the best seedbed for red maple, and a thin layer of hardwood leaf litter does not hinder germination and early survival. Many red maple seeds germinate each year in abandoned old fields, in cutover areas and burns, and in the forest. Reproduction has also been observed on strip-mine spoil banks in Pennsylvania, West Virginia, and Ohio (*26*). Not many new seedlings can survive under a closed forest canopy, but enough do survive to perpetuate the species in abundance.

Presently, red maple is important in many stands where it was formerly a limited associate; it is enabled to increase by disturbances such as disease, windthrow, fire, and harvesting (*5,15,19,37,40*). In southeastern Ohio, 6 years after clearcutting a 3.4 ha (8.5 acre) mature oak-hickory stand, the new stand contained more than 2,200 red maple seedlings per hectare (900/acre) taller than 1.4 m (4.5 ft), together with many yellow-poplar and oak seedlings (Unpub. data, Vinton Furnace Experimental Forest, McArthur, OH). The original stand on the plot contained no red maple. There were occasional red maples in nearby stands. Red maple does not show a strong affinity for either northern or southern exposures (*48*), but its best growth form is often found on northeast slopes (*40*). The young seedlings are shade tolerant, and abundant 1- to 4-year-old seedlings are often found under the canopy of older stands. Many of these seedlings die each year if they are not released by opening of the main crown canopy, but new ones replace them. Thus, a reservoir of seedlings and ungerminated seed is available to respond to increased sunlight resulting from disturbance. Pre-existing red maples in a cut stand add greatly to the new stand stocking through stump sprouts (*21*). In some species, disturbances of small areas often restrict development of new age classes because the canopy over small areas closes in from the side too quickly. Red maple, however, is sufficiently shade tolerant to respond and may increase in prominence after small disturbances (*20,37*).

Red maple shows an early tendency to develop root system characteristics according to soil conditions, enabling it to grow on greatly different sites ranging from swamp to dry upland (*62*). On wet sites, red maple seedlings produce short taproots with long, well-developed laterals. On dry sites, they develop long taproots with much shorter laterals (*26*). Red maple seedlings are classified as moderately tolerant of soil saturation. In one study, their growth was only slightly retarded after 60 days in saturated soils (*24*). Red maple seedlings were very tolerant of flooding, showing no sign of stem or leaf damage after 60 days of flooding (*7*). This capacity to withstand conditions of wetness or dryness enables survival and growth on a wide variety of site conditions where red maple grows naturally.

Throughout the northern portion of its range, with respect to shade, red maple seedlings are rated moderately tolerant to tolerant and are often abundant in the understory advance reproduction. In the Piedmont, red maple seedlings were found to be shade intolerant however; and, in the lower Mississippi Basin, red maple seedlings grow well only in openings. The species was found to be more shade tolerant on good sites than on poor sites. Overall, it ranks more shade tolerant than yellow birch or white ash (*Fraxinus americana*) but less so than sugar maple, American beech, or eastern hophornbeam (*26*).

Sugar maple is one of the first species to start stem elongation in the spring, and red maple starts only a few days later. In one study, red maple stem elongation was one-half completed in 1 week. Growth then slowed and was 90 percent completed in 54 days (*27*). Under favorable light and moisture, red maple seedlings can grow 0.3 m (1 ft) the first year and as much as 0.6 m (2 ft) each year for the next few years. Some sprouts can grow 0.9 m (3 ft) or more the first year (*26*), but they soon slow to about the same rate as seedlings.

Although red maple naturally germinates and becomes established on many types of seedbeds, direct seeding in an old field failed. Survival was only 37 percent after the first year (*2*). Planting of seedlings has not succeeded on strip-mine spoil banks (*26*) or old fields (*45*). First year survival generally is low and survivors may show poor growth rate and form. Planted red maple infected with mycorrhizae may grow somewhat better, especially on strip-mine spoil banks (*10*). In the nursery, red maple seedling growth was increased when 4 hours of supplemental light and an aluminum foil soil mulch were provided, and when the soil was treated with the insecticide Disulfoton. In 1 year, these seedlings compared favorably with 2- to 3-year-old seedlings grown by conventional methods (*8*). If planting of red maple is desired, container-grown stock seems to offer some promise. Ninety-eight percent of the red maple tubelings planted in a New Hampshire forest clearcutting during August survived. The stock had been grown for 8 weeks in containers. Two container sizes—41 cm^3 (2.5 in^3) and 125 cm^3 (7.6 in^3)—were compared, with no difference in results (*17*).

Red maple is a common associate in second-growth cherry-maple Allegheny hardwood stands. But after clearcutting, red maple seedlings often grow poorly, whereas the black cherry seedlings do well. A chemical from black cherry, perhaps benzoic acid, may interfere with red maple development (*22*). Black cher-

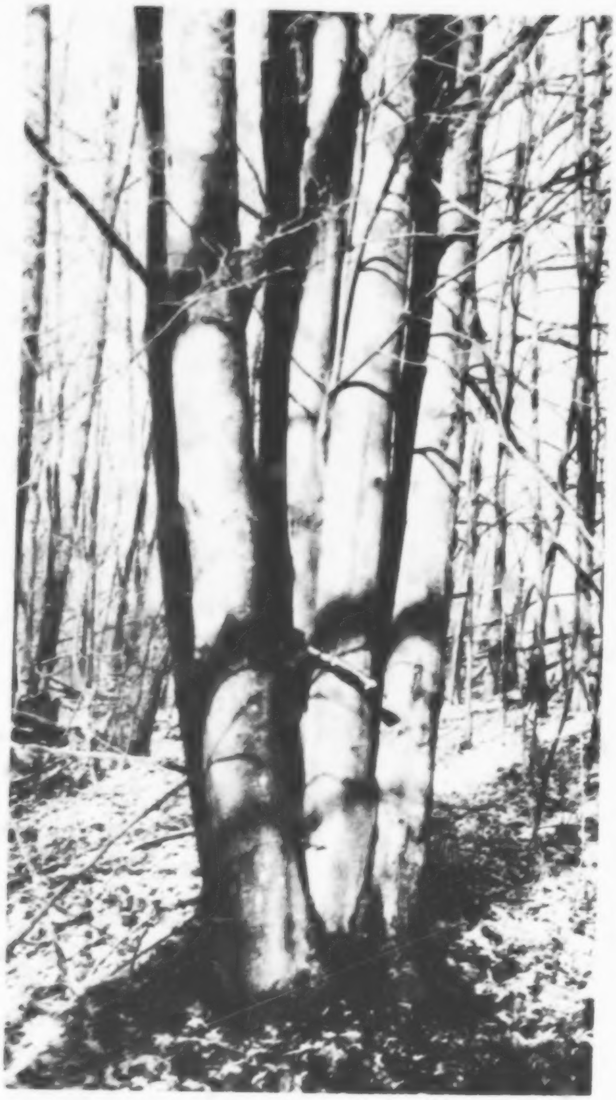

Figure 3—*Clump of red maple stump sprouts.*

ry leaves have been identified as a source of benzoic acid and as a potential allelopathic inhibitor of red maple *(23)*.

Vegetative Reproduction—Red maple stumps sprout vigorously (figs. 3, 4). Inhibited, dormant buds are always present at the base of red maple stems. Within 2 to 6 weeks after the stem is cut, these inhibited buds begin to extend *(65)*. Fire can also stimulate these buds. The number of sprouts per stump increases with stump diameter to a maximum of 23 to 30 cm (9 to 12 in), and then decreases among larger trees. Stumps of younger trees tend to produce taller sprouts *(39,47)*. Sprouts grow faster than seedlings, and leaf and internode size is greater. As competition increases, growth rates slow *(65)*. Many of the sprouts have rot and poor form *(58)*. Also, the attachment of a sprout to the stump is often weak because the base of the sprout grows over the stump bark and the vascular connection between them is constricted *(65)*. Regeneration by seedling sprout may be especially successful *(19)*. Generally, the species' great sprouting capacity makes it suitable for coppicing and accounts for its tendency to be found in sprout clumps.

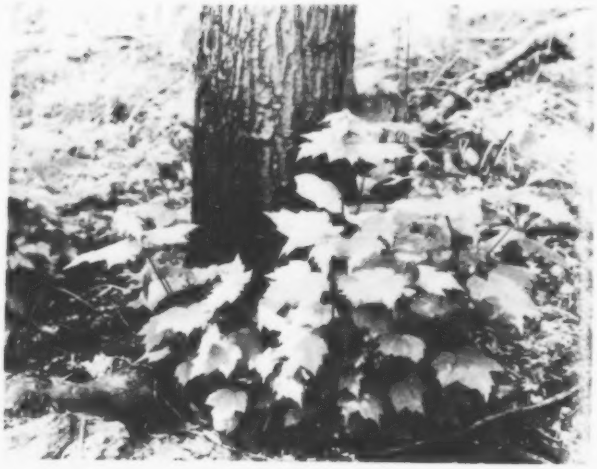

Figure 4—*Red maple sprouts at base of tree 30 cm (12 in) in d.b.h. 2 months after a prescribed burn.*

Red maple is difficult to propagate from cuttings and success varies considerably. Some rooting has been obtained by treating cuttings with a concentration of 200 mg per liter (200 p/m) of indolebutyric acid for 3 hours. Cuttings collected in June seem to root better than those taken later in the growing season. Cuttings from the lower part of the crown root better than those from the upper part, and cuttings from male clones or female clones, which fruit sparingly, root better. Successful bud grafting on an experimental basis has been reported with red maple and with sugar maple on red maple stocks, and layering has been observed in central Pennsylvania. For the most part, however, the species is difficult to propagate vegetatively, except by means of stump sprouts *(26)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Red maple is a short- to medium-lived tree and seldom lives longer than 150 years. It reaches maturity in 70 to 80 years. Average mature trees are 18 to 27 m (60 to 90 ft) in height and 46 to 76 cm (18 to 30 in) in diameter *(26)*. The largest registered living red maple is growing near Armada, MI. It is 38.1 m (125 ft) tall and has a bole circumference, at breast height, of 4.95 m (16.25 ft) *(38)*.

Although red maple height growth starts relatively early in the spring, radial growth starts late in the season. Radial growth then proceeds rapidly, becoming half complete in 50 to 59 days and fully complete in 70 to 79 days. In a New York study, red maple total height growth was somewhat better than that of the other species studied *(26)*.

Growth during early life is rapid but slows after trees pass the pole stage. Red maple responds well to thinning. In upper Michigan, thinning was more effective than fertilization for stimulating red maple growth *(49)*. In the Canadian Maritimes, a 35-year-old coppice red maple stand was thinned by reducing each sprout clump to one of the better stems. The number of red maple stems was reduced from 2,610 to 560/ha (1,057 to 227/acre). Ten years later, these residual trees had more than doubled their volume to 63.8 m^3/ha (911 ft^3/acre). In another study, a partial cutting was made on a 40-year-old stand of Allegheny northern hardwoods. Of all the species, red maple grew best. In the 10-year period after cutting, dominant red maple trees grew an average of 5.7 cm (2.25 in) in diameter. In the north, the young red maple trees grow faster than sugar maple, beech, or yellow birch, but slower than aspen, paper birch, or white ash. In southern bottom lands, the growth rate of red maple compares favorably with that of other hardwood species. An average diameter growth of 7.5 to 9 cm (3.0 to 3.5 in) in 10 years is possible *(26)*.

Early crop tree release of red maple seedlings and sprouts is feasible in young, even-aged stands. It should be done when the new stand has crown closure and crown dominance is being expressed. This occurred on 9- to 12-year-old trees in West Virginia *(56,57)*. Only 10 percent of red maple sprout clumps did not have a sprout of potential crop tree quality *(29)*. Released red maple trees have a low susceptibility to epicormic sprouting *(46)*.

Rooting Habit—Red maple trees grow well and are generally capable of growing as well as or better than their associates on sites with less than optimum moisture conditions, either too wet or too dry. In Michigan, red maple sprouts grew about twice as fast on wet organic soils as on mineral soils or drier organic soils *(26)*. Roots of maple seedlings are capable of developing differently in response to various environments, so that the seedlings can survive in situations ranging from swamp to dry upland. This characteristic root system adaptability is maintained as the trees grow older. Under flood conditions, many adventitious roots develop, but the root systems recover quickly upon drainage *(24)*. Red maples seem to tolerate drought through their readiness to stop growing under dry conditions *(52)* and by producing a second growth flush when conditions improve again, even after growth has stopped for 2 weeks *(27)*.

Red maple roots are primarily horizontal and form in the upper 25 cm (10 in) of soil. After germination, a taproot develops until it is about 2 to 5 cm (1 to 2 in) long, then it turns and grows horizontally. As the woody roots extend sideways, nonwoody fans of feeder roots extend upward, mostly within the upper 8 cm (3 in) of mineral soil. The woody roots may be 25 m (80 ft) long *(34)*. Although red maple trees and seedlings tolerate flooding, they can be damaged if silt and sand layers 7.6 cm (3 in) or more are deposited over their roots *(6)*.

Reaction to Competition—Red maple is a pioneer or subclimax species that is more shade tolerant and longer lived than the usual early successional species, such as poplar (aspen) and pin cherry. It compares in shade tolerance with sycamore *(Platanus occidentalis)*, silver maple, American basswood *(Tilia americana)*, common persimmon *(Diospyros virginiana)*, black gum, and rock elm *(Ulmus thomasii)*. It is not as tolerant as sugar maple, American beech, eastern hophornbeam, and flowering dogwood *(Cornus florida)* *(26)*. Red maple can most accurately be classed as tolerant of shade. Seedlings are more shade tolerant than larger trees and can exist in the understory for several years. They respond rapidly to release and can occupy overstory space. Disturbances such as fire, disease, hurricanes, and harvesting have caused red maple to increase in stocking where it previously occurred as only scattered trees *(19,31,35,40,48,55)*. As these stands mature and the canopy closes, red maple growth slows due to competition for light *(9)*.

Following a hurricane in central New England, the site was soon dominated by pin cherry, with red maple, northern red oak, paper birch, and a few eastern white pine. After 10 years, the pin cherry was giving way to dominance by red maple. After 40 years, however, northern red oak and paper birch had assumed dominance over the the now codominant red maple *(19)*. In northern hardwood types, red maple begins to give way to sugar maple and more tolerant hardwoods after about 80 years *(26)*, but on certain wet sites, red maple can probably maintain itself indefinitely as an edaphic climax *(13)*.

Red maple is generally very resistant to herbicides *(28)*. Also, diffuse porous species such as red maple are difficult to kill by girdling. For example, 3 years after treatment, 70 percent of the girdled trees had live crowns *(63)*. Stem injection, using cacodylic acid *(12)* and picloram *(61)*, did successfully control red maple as did glyphosate applied by hydraulic sprayer, but not when applied by a mist blower *(16)*. Generally, if treatment of red maple is planned, it is wise to consult current labels or experts in the field of chemical control to determine the latest allowable chemicals and the best methods of application.

Damaging Agents—Red maple is generally considered very susceptible to defect. Especially on poor sites, red maple often has poor form and considerable internal defect. Discoloration and decay advance much faster in red maple than in sugar maple *(43)*. In northeastern Pennyslvania, average cull ranged from 13 percent in 30 cm (12 in) diameter red maple trees to 46 percent in 61 cm (24 in) diameter trees. Only associated beech and black birch were more defective *(26)*.

Sprout clumps present some serious problems. More defects originate from branch stubs on the sprout stems than from the parent stump *(43)*. *Inonotus glomeratus* can infect branch stubs and wounds above the butt in red maple. Nevertheless, a red maple sprout with only a slightly defective base and small and well-healed branch stubs has a potential for high future value. Criteria for selecting red maple sprouts for thinning are (1) select only stems with small, well-healed branch stubs, (2) reject sprout clumps with defective bases, and (3) cut all but one or two of the best dominant stem sprouts *(50)*.

Many trunk rot fungi and stem diseases attack red maple. *Inonotus glomeratus* infects branch stubs and wounds on the stem and is most important. Second in importance is *Oxyporus populinus*, which forms a small, white fruit body that often has moss growing on top. *Phellinus igniarius* is another leading heart rot of red maple. Red maple may also be cankered by species of *Nectria, Eutypella, Hypoxylon, Schizoxylon, Strumella*, and others *(18)*.

Red maple is susceptible to many leaf diseases, generally of minor importance. It is seldom or seriously damaged by root diseases, although *Armillaria mellea* can enter through root or butt wounds. However, *A. mellea* kills only trees already weakened from other causes *(18)*.

Mechanical injury is a common source of defect in hardwoods, and red maple is especially sensitive to wounding. Often, large areas of cambium surrounding the wound will die back. In shade tree maintenance, wound dressings have not proven effective in stimulating wound closure or internal compartmentalization of the damaged area *(44)*. Increment boring causes discoloration and may lead to decay in red maple. Callus growth, when established, is reasonably rapid, but an extra year or two often is needed if cambial dieback has been extensive around the wound *(26)*. Red maple was rated intermediate with respect to amount of damage after a severe glaze storm in Pennsylvania. In one study, major damage was sustained by 41 percent of the black cherry, 16 percent of the red maple, and 5 percent of the hemlock *(18)*.

Many different insects feed on red maple, but probably none of them kill healthy trees. They do reduce vigor and growth leaving the tree more susceptible to attack from fungi. Insect feeding also may hasten the death of weakened trees. Susceptibility to insect attack is illustrated by a study in the Piedmont. Of 40 species investigated, red maple had the highest percentage (79 percent) of insect attacks. Among the more important borers attacking red maple were the gallmaking maple borer *(Xylotrechus aceris)*, the maple callus borer *(Synanthedon acerni)*, and the Columbian timber beetle *(Corthylus columbianus)*. The common scale insects included the cottony maple scale *(Pulvinaria vitis)*, the maple leaf scale *(P. acericola)*, and the oystershell scale *(Lepidosaphes ulmi)*. The common leaf feeding moths were the gypsy moth *(Lymantria dispar)*, the linden looper *(Erannis tiliaria)*, the elm spanworm *(Ennomos subsignaria)*, and the red maple spanworm *(Itame pustularia)*. The forest tent caterpillar *(Malacosoma disstria)* avoids red maple, however *(26)*.

Red maple is very sensitive to fire injury, and even large trees can be killed by a fire of moderate intensity. The fire-killed trees sprout vigorously, however, and red maple may become a more important stand component after a fire than before one *(26)*.

Red maple is a desirable deer food and reproduction may be almost completely suppressed in areas of excessive deer populations. Snowshoe hares may also reduce the amount of red maple reproduction *(26)*.

If sapsuckers attack red maple, ringshake may develop *(42)*. Sapsucker damage may also result in mortality. Healthy as well as unhealthy trees are attacked and nearly 40 percent of the trees attacked may be killed *(41)*.

Special Uses

Red maple is known in the lumber industry as soft maple. The wood is close grained and resembles sugar maple but is softer in texture, not as heavy, lacks the figure, and has somewhat poorer machining qualities. Red maple in the better grades is substituted for hard maple, particularly for furniture. Red maple lumber shrinkage from green to oven-dry moisture content is slightly more than shrinkage for hard maple in radial, tangential, and volumetric measurements *(60)*.

Brilliant fall coloring is one of the outstanding features of red maple. In the northern forest, its bright red foliage is a striking contrast against the dark green conifers and the white bark and yellow foliage of the paper birches. Red maple is widely used as a landscape tree.

Although the hard maples—sugar and black maple (*Acer nigrum*)—are principally used for syrup production, red maple is also suitable. When sap and syrup from sugar maple were compared with those of red and silver maple, boxelder (*A. negundo*), and Norway maple (*A. platanoides*), they were found to be equal in sweetness, flavor, and quality *(30)*. The buds of red and silver maple and boxelder break dormancy much earlier in the spring than sugar maple, however, and the chemical content of the sap changes, imparting an undesirable flavor to the syrup. Consequently, the tapping season for red and silver maple is shorter than that for sugar maple.

Red maple is a highly desirable wildlife browse food. Elk and white-tailed deer especially use the current season's growth of red maple and aspen as an important source of winter food *(25)*. Timber harvesting slash can provide an important source of browse to help sustain the animals. Red maple, sugar maple, and paper birch trees cut any time after leaf fall provide browse as nutritious as, and more acceptable than, trees cut immediately before leaf fall *(3)*.

Genetics

As might be expected from its wide range, red maple shows great variation in height, cold hardiness, straightness, time of flushing, onset of dormancy, and other traits. In general, red maples in the north show the most reddish autumn color, earliest flushing and bud set, and least winter injury. Seeds from the north-central and east-central range produce the tallest seedlings. Genetic potential has been found for breeding and selecting red maple against three major urban stresses: verticillium wilt, air pollution, and drought *(52,53)*. Red maple fruits also exhibit geographical variation. The more northerly sources, from locations with short frost-free periods, produced samaras that are shorter but heavier than those from southern sources *(51,66)*.

Experimental crosses of red and silver maple have been made *(26)*. Also, red maple is known to hybridize naturally with silver maple *(33)*.

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Acer saccharinum L. Silver Maple

Aceraceae Maple family

William J. Gabriel

Silver maple (*Acer saccharinum*) is a medium-sized tree of short bole and quickly branching crown common in the Eastern United States where it is also called soft maple, river maple, silverleaf maple, swamp maple, water maple, and white maple. It is found on stream banks, flood plains, and lake edges where it grows best on better-drained, moist alluvial soils. Growth is rapid in both pure and mixed stands and the tree may live 130 years or more. Silver maple is cut and sold with red maple (*A. rubrum*) as soft maple lumber. The winged seeds are the largest of any of the native maple. They are produced in great abundance annually, providing many birds and small mammals with food. An attractive tree with delicate and graceful foliage, silver maple is often planted as an ornamental.

Habitat

Native Range

The natural range of silver maple (figs. 1, 2) extends from New Brunswick, central Maine, and southern Quebec, west in southeastern Ontario and northern Michigan to southwestern Ontario; south in Minnesota to southeastern South Dakota, eastern Nebraska, Kansas, and Oklahoma; and east in Arkansas, Louisiana, Mississippi, and Alabama to northwestern Florida and central Georgia *(22)*. The species is absent at higher elevations in the Appalachians.

Silver maple has been introduced to areas of the Black Sea coast of the Soviet Union, where it has adapted to the growing conditions there and is reproducing naturally in small stands *(24)*.

Climate

The important climatic factors within the area of the natural distribution of silver maple vary as follows: normal annual total precipitation, 810 to 1520 mm (32 to 60 in); growing season precipitation (May, June, July, and August), 200 to 810 mm (8 to 32 in); mean annual snowfall, 0 to 254 cm (0 to 100 in); mean length of frost-free period, 120 to 240 days *(42)*.

There is no information on specific climatic factors that may influence the natural range of silver maple. It is not found in the colder climate of high mountainous areas, and in the drier parts of its range it grows only along streams where ample moisture is available. Its ability to withstand temporary flooding better than other species gives it an advantage in competing for growing space. When planted as ornamentals, trees grow vigorously under a variety of climatic factors from coast to coast.

Soils and Topography

Within the range of silver maple the forest soils are predominantly brown and gray-brown podzols (orders Spodosols and Inceptisols) but the species is found most often on alluvial soils in the orders Inceptisols and Mollisols. Its best growth is in better-drained moist areas *(11)*. On occasions silver maple may occupy low pH (2.2 to 3.3) muck or shallow peat soils (order Histosols), but is not generally found in soils where acidity is below 4.0 *(26)*.

In descriptions of forest vegetation, silver maple appears as a dominant species only in streamside communities or on the fringes of lakes or backwaters of streams. Occasionally it is found in swamps, gullies, and small depressions of slow drainage. Though it generally cannot compete with other species in upland environments, silver maple seedlings are adapted to survive long periods of inundation in bottom lands, where flooding is one of the factors that determine the makeup of individual stands *(11,23)*.

Associated Forest Cover

In the Central Forest Region, Silver Maple–American Elm (Society of American Foresters Type 62) is a major eastern forest cover type *(7)*. In addition to American elm *(Ulmus americana)*, other major associates of silver maple are sweetgum *(Liquidambar styraciflua)*, pin oak *(Quercus palustris)*, swamp white oak *(Q. bicolor)*, eastern cottonwood *(Populus deltoides)*, sycamore *(Platanus occidentalis)*, and green ash *(Fraxinus pennsylvanica)*.

Understory species commonly found with silver maple in the Central Forest Region are willow *(Salix* spp.), redberry elder *(Sambucus pubens)*, red-osier dogwood *(Cornus stolonifera)*, and greenbriar *(Smilax* spp.). Associated herbaceous species are wood-nettle *(Laportea canadensis)*, jewelweed *(Impatiens* spp.), poison-ivy *(Toxicodendron radicans)*, cardinal flower *(Lobelia cardinalis)*, Joe-pye-weed

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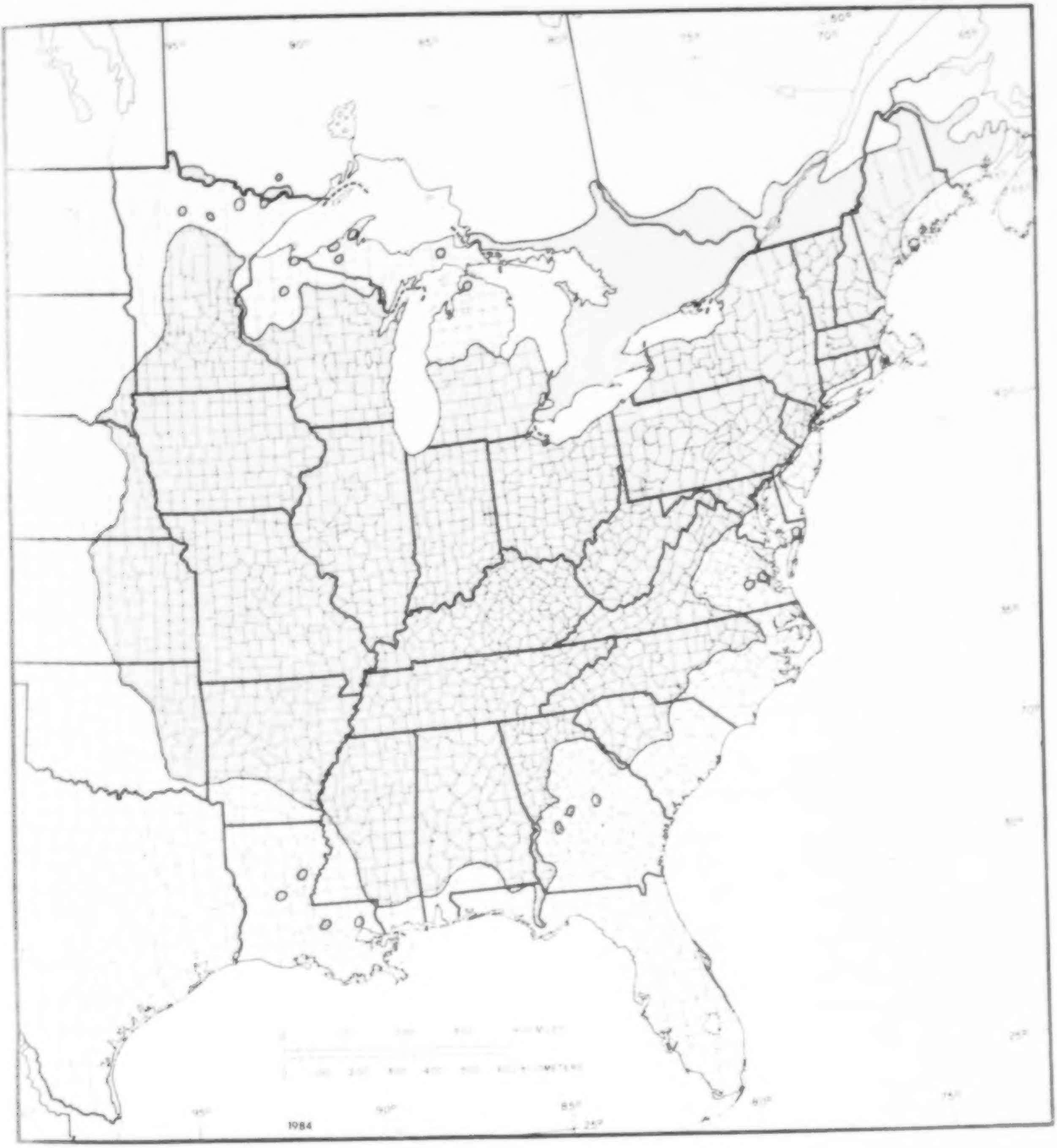
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Figure 1—*The native range of silver maple.*

Figure 2—*Ornamental planting of silver maple.*

(*Eupatorium* spp.), swamp milkweed (*Asclepias incarnata*), and boneset (*Eupatorium perfoliatum*).

In the Northern Forest Region, silver maple in northern Ohio and Indiana is associated with swamp white oak, sycamore, pin oak, black tupelo (*Nyssa sylvatica*), and eastern cottonwood; in New England and eastern Canada with sweet birch (*Betula lenta*), paper birch (*B. papyrifera*), and gray birch (*B. populifolia*); in New York with white ash (*Fraxinus americana*), slippery elm (*Ulmus rubra*), rock elm (*U. thomasii*), yellow birch (*Betula alleghaniensis*), black tupelo, sycamore, eastern hemlock (*Tsuga canadensis*), bur oak (*Quercus macrocarpa*), and swamp white oak.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Silver maple is the first of the maples to bloom in North America, beginning as early as February and extending into May (*38*). Flowers are greenish yellow and bloom long before the leaves appear. They are borne on short pedicels in sessile, axillary fascicles on shoots of the previous year, or on short, spurlike branchlets developed the year before. Separate clusters of female and male flowers appear on the same tree or on different trees (*19,37*).

Four types of trees, with respect to sex expression, have been observed: all male flowers; all female flowers but with rudimentary pistils; mostly male with a few females; and mostly male with a few females and a scattering of hermaphroditic flowers (*19*).

Silver maples growing in Holland showed a tendency for the same tree to produce female flowers one year and both female and male flowers the next year. Trees that produced all male flowers did not show this type of change (*6*).

Fruits and seeds of silver maple develop rapidly. Within 24 hours after pollination flower parts become withered and ovaries begin to swell. Fruits are about 6 mm (0.25 in) long 1 week after pollination. At the end of 3 weeks, when they become mature samaras, the fruits are about 5 cm (2 in) long. Fruit pedicels are short, ranging in length from 2.5 cm (1 in) to nearly 9 cm (3.5 in) (*19*).

Ripening fruits change from a green or rose color to yellowish or reddish brown. Seeds to be placed in storage should be picked when their moisture content is more than 30 percent and should be maintained at this level. Seeds with less than 30 percent moisture content lose their viability quickly.

Seed Production and Dissemination—Seed ripening and dispersal over the range of the species begins in April and ends in June. The number of seed-filled fruits per kilogram ranges from 1,980 to 7,050 (900 to 3,200/lb), with an average of 3,920 (1,780/lb), making these the largest seeds of any maple species in the United States (*38*). Dissemination is mainly by wind and occasionally by water. The minimum seed-bearing age of trees is 11 years.

Seedling Development—Silver maple seeds require no stratification or pretreatment. They are capable of germinating immediately at maturity. When seeds are covered, germination is hypogeal, the cotyledons remaining below ground. This is contrary to evidence reported previously which states that germination of all maples is epigeal (*38*), i.e., where the cotyledons are borne above the surface of the soil. When seeds germinate on bare soil, there is little development of the hypocotyl; the cotyledons shed their fruit coat and spread apart as in epigeal germination *(6)*.

Natural regeneration of young seedlings is most successful on seedbeds of moist, mineral soils with considerable organic matter *(48)*. Seedlings that are established on bottomland sites are often stunted if the soil becomes saturated with water but generally recover when soil moisture drops. When growing in potassium-deficient soils, plants are stunted; young leaves are chlorotic and older leaves are necrotic *(30)*. Initial growth of seedlings may be rapid, ranging from 30 to 90 cm (12 to 36 in) in the first year, but they cannot compete with overtopping vegetation. First-year mortality is high if they are not released.

Seedlings of silver maple require 2,000 to 2,500 hours of chilling to break dormancy. No differences were found in the time of first budbreak between cold-stored and nursery-lifted stock; there is a strong correlation between time of first budburst and root regeneration after the seedlings are transformed to environmental conditions suitable for growth. Maximum root regeneration takes place after 3,500 hours of chilling, but new roots can develop from November to May *(47)*.

The preferred size of seedlings for establishing plantations of silver maple in Ontario is 30 cm (12 in) in height and 6 mm (0.25 in) in root-collar diameter *(43)*.

Vegetative Reproduction—Silver maple can be propagated vegetatively. Softwood cuttings taken in July and again in October rooted 100 percent and 92 percent, respectively *(34)*. Hardwood cuttings taken in early winter and stored in a cool place for 2 months rooted 84 percent when planted in moist sand *(13)*. The treatment of silver maple cuttings with rooting hormones may be important to rooting success *(18)*. Cuttings taken from young trees (5 years of age) root easily, but cuttings from mature trees (80 years old) root very poorly.

Success in bud grafting is mixed. Graft-takes among clones may range from 0 to 40 percent when the branches from which bud sticks are collected have lateral, epicormic, and coppice origins. A high degree of success was recorded for bud grafts of the hybrid red maple × silver maple made on 4-month-old silver maple seedlings *(48)*.

Layering has been used successfully to propagate the species. Horizontally oriented stems have greater rooting success than vertical stems. Although layering occurs without hormone treatment, maximum results are obtained from treated stems. Prolific sprouting from the root collars and lower stems of living trees is characteristic of the species. Sprouts appear readily from stumps that are 30 cm (12 in) or less in diameter.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth of young trees is seriously affected by competition from other vegetation. Height growth averaged 3.8 m (12.5 ft) after five growing seasons under plantation conditions where site preparation was intense and weed control was complete *(44)*. With no site preparation, the average height of trees of the same age was only 0.5 m (1.6 ft). Seedling growth is increased by the application of 56 g (2 oz) in slow release packets of 19-5-17 (N-P-K) fertilizer at the time of planting *(1)*.

Growth in d.b.h. of pole-size trees increased from 6 mm (0.25 in) to 13 mm (0.5 in) following a stand thinning to a 5.2 m (17 ft) spacing. Basal area of the crop trees nearly doubled and wood volume tripled during a 10-year period following thinning. Unthinned stands had only one-third of the basal area and two-thirds of the volume of thinned stands during the period *(18)*.

Silver maple grows rapidly in both pure and mixed stands, some trees growing from 13 mm (0.5 in) to nearly 25 mm (1 in) in d.b.h. each year *(18)*. Plantation silver maples (fig. 3) in southern Ontario averaged 25 m (81 ft) in height and 29.7 cm (11.7 in) in d.b.h. at 43 years of age *(45)*. One tree in Vermont consistently grew 5 cm (2 in) in diameter each year. Mature trees have reached a height of 26 to 37 m (90 to 120 ft) with a trunk diameter of 91 to 122 m (36 to 48 in) *(37)*.

Since the species is usually found in mixed hardwood stands, data on yields for silver maple alone are not available.

Rooting Habit—The species has a shallow, fibrous root system. Survival would be enhanced by this system rather than one that is deep and taprooted, since silver maple is primarily found on the more protected floodplain and bottom-land sites. Its prolific root system is notorious for invading and clogging underground drainage and water lines that are not tightly constructed.

Reaction to Competition—The tolerance to shade of silver maple ranges from moderately tolerant to very intolerant, depending on site quality and location. In general, it is considered tolerant on good sites and almost intolerant on poor sites *(48)*. Foresters, in general, class silver maple as tolerant of shade *(2)*, but the species has been rated very intolerant on bottom-land sites in the South *(48)*. Seedlings are intermediate in tolerance to water-saturated soils *(12)* but can tolerate prolonged periods of inundation. On upland soils silver maple grows well but is highly intolerant of competing vegetation.

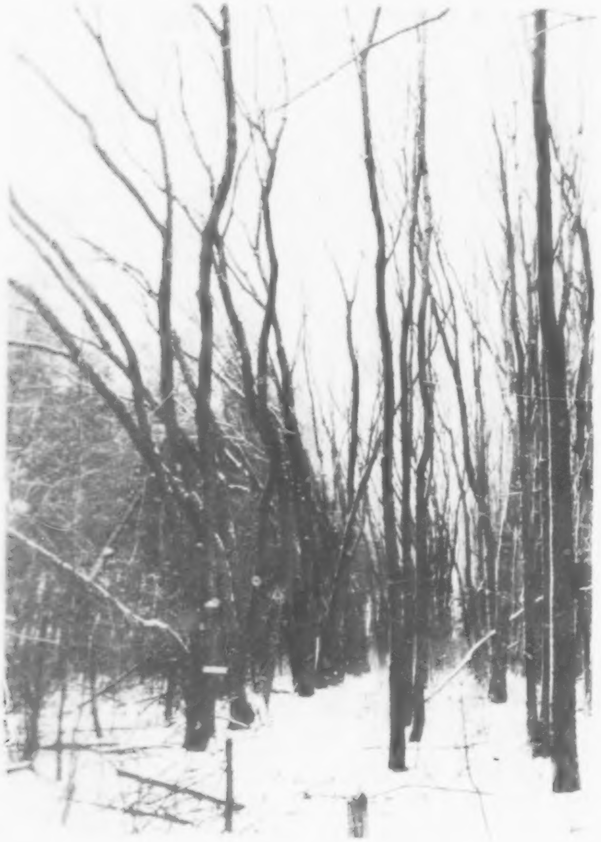

Figure 3—*13-year-old silver maple plantation in southern Ontario. (Courtesy of F. W. von Althen, Canadian Forestry Service).*

Damaging Agents—A number of diseases, insects, and other damaging agents attack the species. Their effect ranges from an unsightly appearance to the weakening and death of the tree.

Chief among the foliage diseases on silver maple are gray-mold spot *(Cristulariella depraedens)*; bull's eye spot *(C. pyramidalis)*, which can cause severe defoliation of nursery stock; anthracnose *(Gloeosporium apocryptum* and *G. saccharinum)*; tar spots *(Phyllosticta minima, Rhytisma acerinum*, and *R. punctatum)*; leaf blister *(Septoria aceris* and *Taphrina carveri)*; and the powdery mildew fungi *(Phyllactinia guttata* and *Uncinula circinata)*. Of less importance are the common spot fungi *Venturia acerina* and *Cladosporium humile (10)*.

Probably the most important stem disease in silver maple is Verticillium wilt *(Verticillium albo-atrum)*, which can cause sudden death. Other diseases of the stem that have either a secondary or parasitic effect are the target canker *(Nectria galligena* and *N. cinnabarina)*, the common mistletoe *(Phoradendron serotinum)*, crown gall *(Agrobacterium tumefaciens)*, and two that produce the brown felty covering over scale insects *(Septobasidium burtii* and *S. pseudopedicellatum) (10)*. The Eutypella canker *(Eutypella parasitica)*, formerly thought to attack only sugar and red maple, has been found on silver maple *(9)*.

A host of root and trunk rots attack silver maple. Seedlings are killed by *Rhizoctonia solani* and the imperfect stage of the charcoal root rot *(Macrophomina phaseoli)*. Shoestring root rot *(Armillaria mellea)* is common on the species and kills trees that are already in a weakened state. A similar root rot *(Armillaria tabescens)* attacks silver maple in the South. A number of other decay fungi act on heartwood and inner sapwood. These are primarily in the *Fomes* and *Hydnum* genera. Flowers and seeds of the species are lost through the discomycete *Ciboria acerina (10)*.

There are no serious insect pests of silver maple, but the species is attacked by borers, leaf feeders, and scale insects. Among the borers are the Columbian timber beetle *(Corthylus columbianus)*; the flatheaded appletree borer *(Chrysobothris femorata)*; the maple callus borer *(Synanthedon acerni)*; and the pinhole borer *(Xyloterinus politus)*. Leaf feeders are the fruittree leaf roller *(Archips argyrospila)*; the cecropia moth *(Hyalophora cecropia)*; and the white-marked tussock moth *(Orgyia leucostigma)*. Bladder gall mites found on the species are *Vasates quadripedes* and *V. aceris-crummena (3,4,46)*. An outbreak of the cottony maple scale *(Pulvinaria innumerabilis)* was controlled by treatment with large numbers of the coccinelid *Hyperaspis signata (25)*. Gypsy moth *(Lymantria dispar)* is not a significant pest of silver maple; the young larvae cannot become established on the species *(27)*.

Silver maple, because of its brittle wood properties, is highly susceptible to ice damage *(5)*; when planted as an ornamental along streets it can be seriously affected by illuminating gas leakage from underground mains. It is known to react unfavorably to certain other air pollutants *(14,15,16,17,41)*.

Special Uses

The buds of silver maple provide a vital link in the food chain of squirrel populations *(33)*. The early swelling and budburst characteristics of the species come during the critical late winter-spring period when stored food supplies of squirrels are exhausted.

Local studies conducted on floodplains in the province of New Brunswick show that the species ranks far above other dominants on wet, mesic sites as nesting trees for wood ducks and goldeneye ducks *(31)*.

Silver maple ranks high as a food source for beavers in southeastern Ohio *(29)*. According to availability, it is exceeded only by common alder in importance.

The species is heavily planted as an ornamental in the urban areas of this country. Its widespread popularity is due to its early rapid growth and its pleasing appearance. Five ornamental subdivisions or forms are recognized in silver maple on the basis of leaf structure, coloration, and habit: (1) *Acer saccharinum laciniatum*—leaves are deeply cleft with leaf lobes that are dissected and narrow; (2) *A. s. tripartitum*—leaf lobes are divided almost to the base of the leaf; (3) *A. s. lutescens*—when the leaves unfold they are yellow-bronze; (4) *A. s. pendulum*—branches are pendulous, hanging or droopy in appearance; and (5) *A. s. pyramidale*—branches are acutely angled from the tree trunk, upright in habit, forming a crown that is narrow and pyramidal in shape *(32,37)*. The U.S. National Arboretum published a checklist of cultivars of silver maple based on the International Code of Nomenclature for Cultivated Plants *(36)* and included 58 names. In the fall of the year the leaves of silver maple change to a soft yellow.

Silver maple has been planted as a farmstead windbreak in several locations in Minnesota. Its survival over a period of 38 years averaged 70 percent. Its height and diameter growth during the period averaged 11.6 m (38 ft) and 17.8 cm (7 in), respectively *(39)*.

In Ontario, tests of five maple species indicated that the quality of syrup from silver maple sap is satisfactory. Sugar content of silver maple sap ranked lowest of the five species tested *(21)*.

There have been no studies of population differences and racial variation in silver maple, possibly because of higher priorities currently given to other, more commercially important hardwoods.

Genetics

A program for the genetic improvement of the species for timber production is in progress in Ontario. Phenotypes with superior form, growth rate, and wood quality have been selected and are being evaluated *(18)*. There are obvious differences in branchiness in seedlings from different silver maple trees within the same stand. These and other observations indicate that sometimes there is enough genetic variability to warrant selection *(49)*.

Because the blooming periods of silver and red maple overlap, there is a possibility of natural hybridization between them. Under controlled artificial conditions, the two species hybridize easily, producing prolific seed sets *(8)*. The hybrids are intermediate between their parents in leaf characters. Their growth was much faster than that of red maple seedlings but did not equal that of silver maple. Hybrids first flowered at 6 years of age, but of several thousand flowers, only a few dozen fruit were produced, indicating incompatibilty between hybrid females and existing pollen sources.

Silver maple crosses readily with red maple when the latter is used as a female parent. But the reciprocal cross gives mixed results: some female silver maples set very few seeds when crossed to red maple while others apparently do very well *(20,28)*. The species also is capable of setting viable seed to self-pollination.

The basic chromosome count in silver maple is $n = 26$. Meiosis takes place in the fall, in contrast to other local maple species whose pollen matures in the spring *(35,40)*. No serious abnormalities of meiosis resulting from hybridity between red and silver maple were reported, except in one cross where $2n = 71$ and 72 instead of $2n = 78$.

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Acer saccharum Marsh. Sugar Maple

Aceraceae Maple family

Richard M. Godman, Harry W. Yawney, and Carl H. Tubbs

Sugar maple *(Acer saccharum)*, sometimes called hard maple or rock maple, is one of the largest and more important of the hardwoods. It grows on approximately 12.5 million hectares (31 million acres) or 9 percent of the hardwood land and has a net volume of about 130 million m^3 (26 billion fbm) or 6 percent of the hardwood sawtimber volume in the United States. The greatest commercial volumes are presently in Michigan, New York, Maine, Wisconsin, and Pennsylvania *(53)*. In most regions, both the sawtimber and growing stock volumes are increasing, with increased production of saw logs, pulpwood, and more recently, firewood.

Habitat

Native Range

The northern limit of sugar maple (figs. 1, 2) nearly parallels the 35th mean annual isotherm extending eastward from the extreme southeast corner of Manitoba, through central Ontario, the southern third of Quebec and all of New Brunswick and Nova Scotia. Within the United States the species is found throughout New England, New York, Pennsylvania, and the middle Atlantic States, extending southwestward through central New Jersey to the Appalachian Mountains, then southward through the western edge of North Carolina to the southern border of Tennessee. The western limit extends through Missouri into a small area of Kansas, the eastern one-third of Iowa, and the eastern two-thirds of Minnesota. A few outlier communites are found in northern Kansas, Georgia, and the Carolinas.

Climate

Sugar maple is restricted to regions with cool, moist climates. In northern areas, January temperatures average about –18° C (0° F) and July temperatures about 16° C (60° F). In the southern portions of the range, January temperatures average about 10° C (50° F) and July temperatures approach 27° C (80° F), although moisture and aspect influence these extremes. In the sugar maple region, typical ranges in temperatures are from –40° C (–40° F) in the north to 38° C (100° F) in the southwestern areas Occasional extremes may be more than 11° C (20° F lower or higher than these.

Precipitation averages range from about 510 mm (20 in) annually near the western edge of the range to 2030 mm (80 in) in the southern Appalachians Much of the northeastern region receives about 1270 mm (50 in) per year where substantial commercia volumes of sugar maple are located. In general, the growing season precipitation is well distributed and averages 380 mm (15 in) in the western areas and 1020 mm (40 in) in the East. Snowfall often exceeds 2540 mm (100 in) in the northern portion of the range.

In the broad geographic area covered by sugar maple, the growing season ranges from 80 to 260 days. The last killing frost usually occurs from March 20 to June 15 and the first killing frost occurs between September 1 and November 10. In mountainous areas of the Northeast, climatic factors largely determine the upper elevation limits of the species *(97)*.

Soils and Topography

Sugar maple grows on a wide variety of sites ranging from a site index of about 12 m (40 ft) to nearly 24 m (80 ft) at age 50 *(12,17,21,25,46,91)*. Typical good quality second-growth stands usually fall between site index 17 and 20 m (55 and 65 ft) for sugar maple at base age 50 years. Height growth is slower after age 50 in the eastern regions. Except on the best sites, the depth of the soil and type of parent material has a marked influence on site index *(69)*.

Sugar maple grows on sands, loamy sands, sandy loams, loams, and silt loams but it does best on well-drained loams *(30)*. It does not grow well on dry, shallow soils and is rarely, if ever, found in swamps *(30)*. Sugar maple is soil-site specific in southerly regions but abundant on a wide variety of soils in the northern Lake States. It is mostly found on Spodosols, Alfisols, and Mollisols among the soil orders. In New Hampshire, sugar maple is associated with sites that have abundant organic matter *(69)*, and in West Virginia it is most abundant on areas with high oak site indices *(107)*.

Sugar maple grows on soils ranging from strongly acid (pH 3.7) to slightly alkaline (pH 7.3), but it most commonly grows on soils with a pH of from 5.5 to 7.3 *(30)*. The heavy leaf litter typical of sugar maple

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tends to modify the pH and nutrient status of the soil. The leaves contain about 1.81 percent calcium, 0.24 percent magnesium, 0.75 percent potassium, 0.11 percent phosphorus, 0.67 percent nitrogen, and 11.85 percent ash, based on dry weight. The pH of leaves ranges from 4.0 to 4.9. The calcium content remains relatively uniform in trees growing with a pH range of 4.5 to 7.0 but drops as the soils become more acid *(5)*.

In the Lake States, sugar maple is found at elevations up to 490 m (1,600 ft)—most commonly on ridges between poorly drained areas and on soil with at least 1 to 1.5 m (3 to 5 ft) to the water table. In northern New England and New York State it grows at elevations up to 760 m (2,500 ft). In the Green

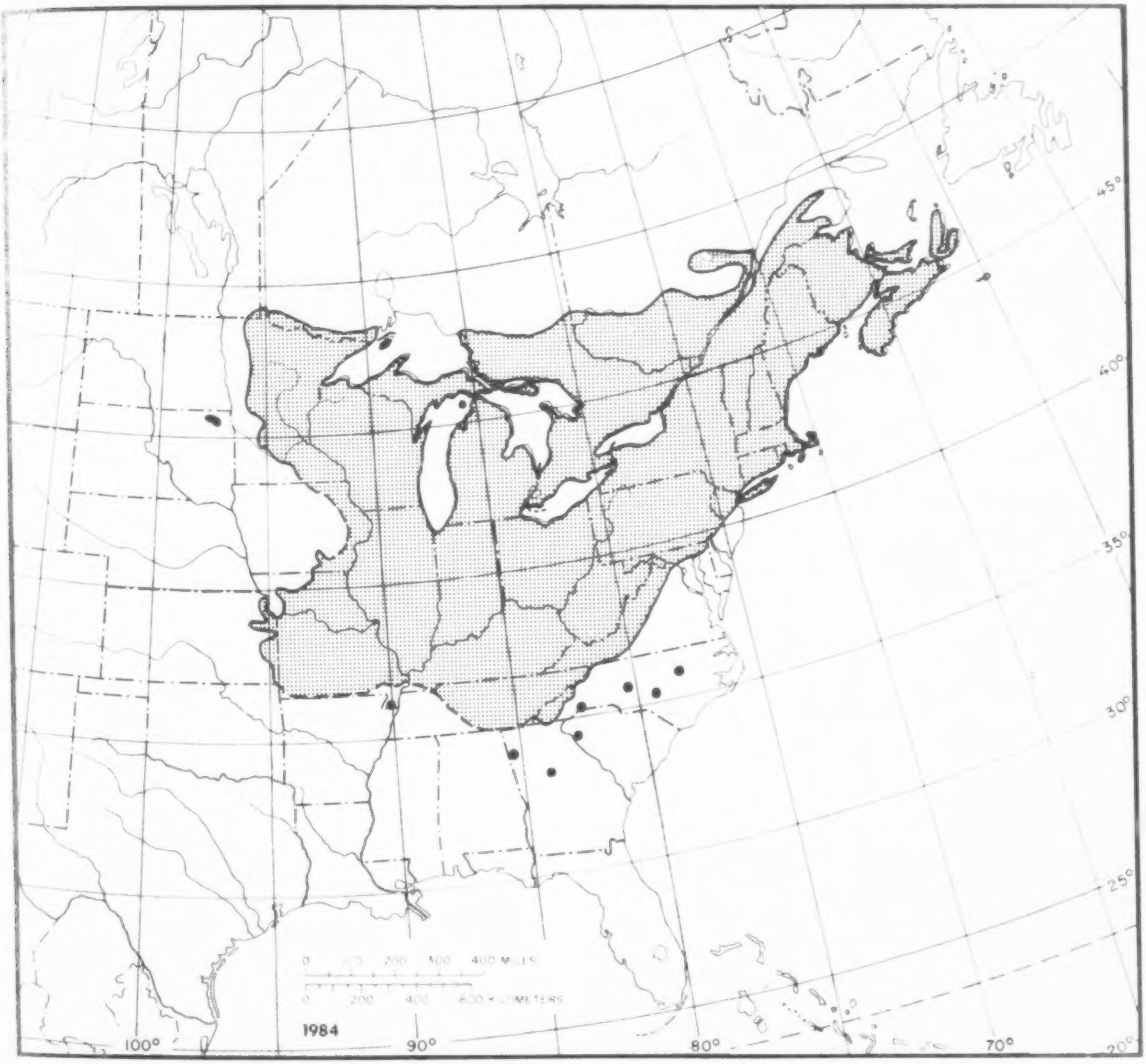

Figure 1—*The native range of sugar maple.*

Mountains of Vermont and the White Mountains of New Hampshire, especially, the upper limit lies in a sharp horizontal band with a narrow transitional zone into the Boreal forest types. In the southern Appalachians the upper elevation ranges from 910 m (3,000 ft) to 1680 m (5,500 ft), with the lower levels generally restricted to the cooler north slopes. In the southern and southwestern parts of its range, sugar maple more typically grows on moist flats and along ravines at intermediate elevations in the rolling topography.

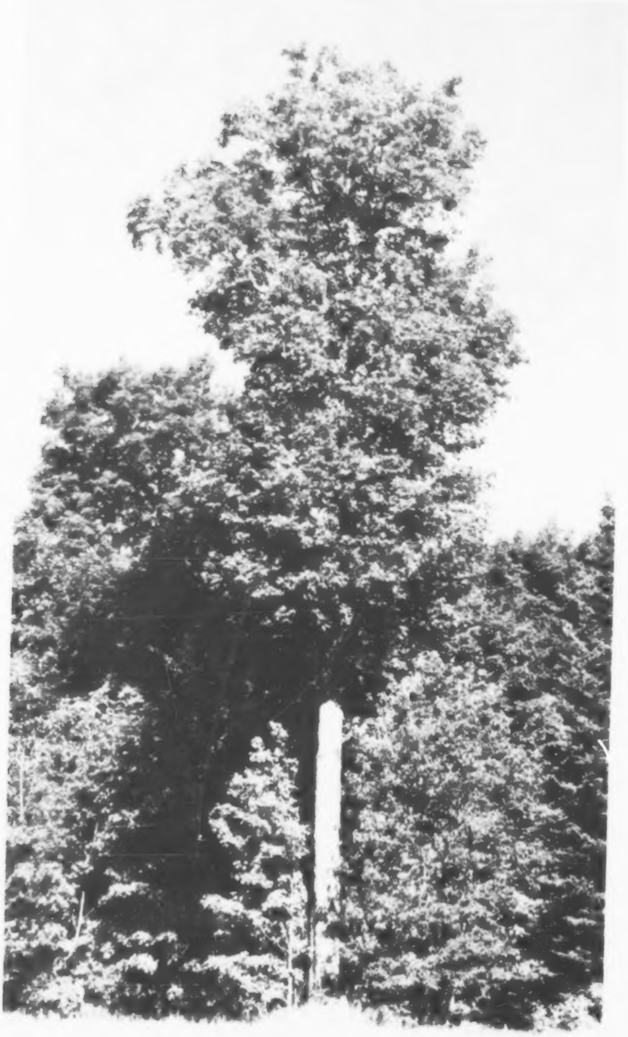

Figure 2—*Sugar maple.*

Associated Forest Cover

In eastern North America sugar maple is a major component in 7 Society of American Foresters forest cover types, a common associate in 17, and an infrequent species in 10 *(20)*.

Sugar maple is a major component in the following types:

27	Sugar Maple
26	Sugar Maple–Basswood
25	Sugar Maple–Beech–Yellow Birch
60	Beech–Sugar Maple
28	Black Cherry–Maple
31	Red Spruce–Sugar Maple–Beech
16	Aspen (Canadian subtype)

Sugar maple is a common associate in the following types:

17	Pin Cherry
107	White Spruce
32	Red Spruce
30	Red Spruce–Yellow Birch
35	Paper Birch–Red Spruce–Balsam Fir
21	Eastern White Pine
22	White Pine–Hemlock
23	Eastern Hemlock
20	White Pine–Northern Red Oak–Red Maple
24	Hemlock–Yellow Birch
108	Red Maple
19	Gray Birch–Red Maple
55	Northern Red Oak
57	Yellow-Poplar
58	Yellow-Poplar–Eastern Hemlock
59	Yellow-Poplar–White Oak–Northern Red Oak
64	Sassafras–Persimmon

It occurs as an infrequent species in Jack Pine (Type 1), Balsam Fir (Type 5), Aspen (Type 16), Red Spruce–Balsam Fir (Type 33), Red Spruce–Fraser Fir (Type 34), Chestnut Oak (Type 44), Pitch Pine (Type 45), White Pine–Chestnut Oak (Type 51), White Oak–Black Oak–Northern Red Oak (Type 52), and River Birch–Sycamore (Type 61).

Large numbers of shrubs are found with sugar maple because of its varied altitudinal distribution. The most common within the commercial range are beaked hazel *(Corylus cornuta)*, Atlantic leatherwood *(Dirca palustris)*, redberry elder *(Sambucus pubens)*, American elder *(S. canadensis)*, alternate-leaf dogwood *(Cornus alternifolia)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, Canada yew *(Taxus canadensis)*, red raspberry *(Rubus idaeus)*, and blackberries *(Rubus* spp.). Common flowering plants include springbeauty *(Claytonia caroliniana)*, large-flowered trillium *(Trillium grandiflorum)*, anemone *(Anemone* spp.), marsh blue violet *(Viola cucullata)*, downy yellow violet *(V. pubescens)*, Solomons-seal *(Polygonatum pubescens)*, false Solomons-seal *(Smilacina stellata)*, sweet cicely *(Osmorhiza* spp.), adderstongue *(Ophioglossom vulgatum)*, jack-in-the-pulpit *(Arisaema atrorubens)*, clubmosses *(Lycopodium* spp.), and largeleaf aster *(Aster macrophyllus)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sugar maple trees seldom flower until they are at least 22 years old; flowering is heavier at later ages. The flower buds usually begin to swell at or slightly before the leaf buds show activity and reach full bloom 1 to 2 weeks before leaves emerge. Flowers appear between late March and mid-May, depending on the geographic location *(85)*.

Flowering in sugar maple is polygamous, occurring over the entire crown. The long-pedicelled, apetalous yellow flowers, about 6.4 cm (2.5 in) long, seem to be perfect, but usually only one sex is functional within each flower. Both sexes are typically produced in the upper part of the crown but only males form in the lower part *(26)*. In some trees, certain major limbs produce only male and others only female flowers. The flowers of sugar maple were thought to be bee-pollinated *(30,64)*, but a recent study showed that pollination occurs freely in sugar maple without the aid of insects *(28)*.

The fruit, a double samara, ripens in about 16 weeks. Usually only one of the paired samaras is filled with a single seed, typically averaging 7 to 9 mm (0.3 to 0.4 in) in length, but occasionally both samaras will contain seed or both will be empty. Some trees produce triple samaras and others produce samaras with double wings. Samaras collected from trees having the bird's-eye wood grain characteristic showed a consistency of overlapping of the wings, a strong union between samaras, and lighter colored wings after drying but these characteristics have not been confirmed as being an attribute associated with bird's-eye *(32)*.

Seeds are mature when the samaras turn yellowish green and have a moisture content less than 45 percent *(11,124)*. The samaras begin falling about 2 weeks after they ripen, usually just before the leaves fall.

Seed Production and Dissemination—The fruit of sugar maple is intermediate in size among species within the genus. Samaras average about 15,400/kg (7,000/lb), but range from 7,060 to 20,070/kg (3,200 to 9,100/lb) *(85)*. The large papery wings, typically 20 to 27 mm (0.8 to 1.1 in) in length and 7 to 11 mm (0.3 to 0.4 in) wide, permit the samara to be carried at least 100 m (330 ft) by the wind. During a good seed year in northern Michigan, 173,000 samaras per hectare (70,000/acre) fell in the center of a 4-ha (10-acre) clearcut *(31)*. Samaras containing seed can be readily separated from empty samaras by immersion in N-pentane. Immersion up to 1 hour may delay germination but has no effect on seed viability *(124)*.

Light fruit crops are produced by 40- to 60-year-old trees with 20 cm (8 in) d.b.h., and moderate crops by 70- to 100-year-old trees with 25- to 36-cm (10- to 14-in) d.b.h. Saw-log-size trees produce vast numbers of samaras. During an excellent fruiting year in northern Michigan, a series of traps caught 22 million/ha (8.56 million/acre) sugar maple samaras in a virgin stand and 11 million/ha (4.3 million/acre) in a selectively cut stand *(30)*.

Based on 32 years of observation in north–central Wisconsin, good or better fruit crops occurred about 44 percent of the years, the lowest percentage among the major hardwood species of the area *(37,40)*. Good or better fruit crops occurred as often as 4 successive years, but successive poor crops did not extend longer than 2 years. The period between good or better crops ranges from 1 to 4 years in north–central Wisconsin, from 2 to 5 years in other portions of the United States, and from 3 to 7 years in Canada *(30,47,115)*.

To germinate, sugar maple seeds require moist stratification at temperatures slightly above freezing for 35 to 90 days. Each sugar maple seed seems to have its own stratification-period threshold, short of which the epigeal germination process ceases *(126)*. Both moisture content and temperature affect how long seeds can be stored. Under proper conditions seeds have been stored for at least 5 years without loss of viability *(10)*. In natural stands, few if any seeds remain viable on the forest floor beyond the first year *(73)*.

Sugar maple seed has an extremely high germination capacity, with averages of 95 percent or more *(126)*. The optimum temperature for germination is about 1° C (34° F), the lowest of any known forest species *(39,108)*. Germination drops rapidly as temperatures increase, and little if any germination occurs above 10° C (50° F). Rapid warming of the surface soil in the spring of 1978 in northern Wisconsin, for example, prevented germination from the bumper seed crop of 1977, except in a few remaining snowbanks along the roads *(38)*. Under natural conditions the cotyledon leaves are out and growing before the snow is gone in the northern regions. This unique characteristic of germination at low temperatures probably accounts for the abundance of sugar maple regeneration under most stand conditions in the north. Another major characteristic of the germinating sugar maple seed is its vigorous development of a strong radicle that has the strength and length to penetrate heavy leaf litter and reach mineral soil during the moist period.

Seedling Development—Seedlings of sugar maple are very shade tolerant and can survive long periods of suppression. In a study of seedling height for 5 years after germination under low lath shade in central Ontario, the tallest seedlings were found under about 65 percent shade, averaging about 127 cm (50 in) tall *(34,71)*. Heights were greater than 102 cm (40 in) from about 35 to 90 percent of full sunlight, with average heights decreasing at more open and heavier shading. A significant finding in this study was that supplemental watering was necessary for survival at more than 55 percent of full sunlight. Dry weight and root development were little affected by the level of light. A Vermont study of shade levels showed no significant difference in seedlings grown under 0, 30, and 60 percent shade but found a marked decrease in development under 90 percent shade. Seedlings grown under the different shade treatments showed no difference, however, in either height or diameter growth 4 years after field planting *(125)*.

Sugar maple roots release an exudate that can inhibit the growth of yellow birch when the root growth periods coincide, thus gaining a growth advantage over one of its associated species *(110)*. Other tree species may be similarly affected. Aster and goldenrod exert an allelopathic effect on sugar maple by reducing germination and early growth of seedlings *(24)*.

The growth of understory seedlings begins before the overstory leafs out, generally about mid-May in Upper Michigan. About 90 percent of the seasonal height growth occurs within 18 days under dense stands and 24 days in the open *(50)*. The major growth of other species studied extended about three times longer.

Seedling numbers greater than 370,500/ha (150,000/acre) are common, although as many as 50 percent of the new seedlings may not survive the first year. Seedlings in the understory of young, dense stands may not survive for more than 5 years but many of the seedlings under stands averaging 25 cm (10 in) d.b.h. or more will persist, although they will have little annual height growth until released. In a study of reproduction in old growth stands cut to various basal area densities, number of seedlings per hectare did not differ significantly at either 2 or 5 years after cutting. After 10 years, seedlings under the lightest overstories (6.9 m^2/ha or 30 ft^2/acre) grew most rapidly although seedlings were abundant under all overstory densities *(109)*.

In the drier Lake States region, natural seedlings must have overstory shade for survival until they reach 0.6 to 1.2 m (2 to 4 ft) in height, at which time their root systems have developed from the litter-mineral soil interface into mineral soil. The entire overstory can then be removed with high seedling survival and full stocking *(42)*. Removing the overstory before seedlings are established usually results in semipermanent wildlife openings in the Lake States *(112)*. In partially cut stands, the tallest seedlings usually develop and constitute the trees of the new stand as the overstory is gradually removed *(78)*.

Planting or other special regenerative measures are rarely needed for sugar maple in New England or the Lake States where the tree grows naturally. In other regions, sugar maple is less aggressive and planting is a desirable practice. Nursery stock used in planting is usually fall sown at a depth of about 6 mm (0.25 in) and covered with about 6 mm (0.25 in) of sawdust. The nursery bed is covered by about 50 percent lath shade. Sowing density should yield about 130 to 160 seedlings per square meter (12 to 15 seedlings/ft^2) and seedlings should be vertically root pruned before lifting, usually as 2-0 stock *(101,121,124)*. On more difficult sites 3-0 stock is preferred with tops averaging about 25 cm (10 in) or about twice the height of 2-0 seedlings *(101)*.

Open field plantings with sugar maple have a high survival rate, but seedlings grow poorly because of their inability to compete for moisture and nutrients with herbaceous vegetation. Generally, open field plantings require good stock and several years of site maintenance to assure success *(114,127)*. Time of planting is important. Survival and growth can be vastly improved by planting very early in the spring compared to planting late in the spring. The increase is attributed to the greater root regeneration capabilities during that time *(118)*. Fall plantings have been highly successful in Vermont *(127)*. Sugar maple must be planted at relatively close spacings in order to correct the forking problems that result from the frequent loss of the terminal bud in this opposite-branched species *(78,89)*.

Vegetative Reproduction—Sugar maple reproduces by stump sprouts and will occasionally layer *(22)*. Root suckering is rare. Seedlings broken during logging readily sprout from dormant buds on the lower bole and quickly regain the height of undamaged seedlings *(52)*. Initial deformities, primarily crook, and stem losses from deer browsing are rapidly overgrown and corrected without development of internal rot *(51)*.

In older stands, the percentage of stumps sprouting decreases with increase in tree size, stand density, and years since cutting. Two years after a cutting in northern Michigan, the most sprouting occurred on 15-cm (6-in) trees and the least sprouting on 76-cm (30-in) trees. The percent of stumps sprouting averaged 94 and 38, respectively. Five years after cutting, the percent of sprouting dropped to about 58 and 6, respectively. The number of sprouts per stump also declined with years since cutting *(30)*. Sugar maple is a prolific sprouter in the North, but it sprouts less than other hardwood species in the southern part of its range *(9,86,88,99)*.

Cuttings of sugar maple can be rooted but may later fail due to poor overwintering survival. Cuttings can be successfully overwintered by forcing the cutting to break bud and produce a flush of new growth immediately after it roots with the use of gibberellic acid *(128)*. Rooting response varies greatly between clones—differences range from 0 to 100 percent, and rooting response tends to be consistent from year to year. Timing the collection of cuttings is critical; those taken in mid-June generally give the best results. A rooting medium consisting of a 1 to 1 mixture of perlite and sphagnum moss, with intermittent misting, has worked well with sugar maple cuttings. The reliability of cuttings to propagate trees with figured wood, such as curly grain and bird's-eye, has not been verified *(30)*.

Sugar maple trees with desirable genetic characteristics can be reproduced by grafting. Success with this method can be highly variable depending to a large degree on grafting techniques, that is, when and under what conditions the scions were collected and handled, treatment of the rootstock, and experience of the grafters *(129)*. Of the various methods available, bud grafting is used most commonly and with a high degree of success by commercial nurserymen *(64)*.

Air-layering, a method of propagation that stimulates root development on branches still attached to the parent tree, is another method that has been successfully used *(16)*. A major disadvantage of this procedure is that branches on some trees selected for propagation may not be readily accessible.

Sapling and Pole Stages to Maturity

Growth and Yield—Early growth of sugar maple is slow, partly because it regenerates under heavy shade. In natural stands, the younger seedlings are sensitive to surface moisture conditions because they have a shallow, fibrous root system that lies between the litter-mineral soil interface of typical podzols. With a gradual increase in light, the root systems penetrate deeper into the mineral soil and height growth increases.

Growth during the pole stage is slower than for most associated hardwood species. Height and radial growth begins at about the same time as the buds leaf out. Height growth is completed in about 15 weeks and radial growth in from 14 to 17 weeks, depending on the season and locality *(30)*. In some areas, height growth is about 85 percent complete within 5 weeks and cambial growth is about 80 percent complete in 8 weeks *(30)*.

In the Lake States, older sugar maple trees (fig. 3) in a mature stand grew 2.5 cm (1 in) d.b.h. in 10 years *(30)*. Maximum diameter growth rates of individual trees in mature stands in the Upper Peninsula of Michigan were about 7.6 cm (3 in) per decade for 46-cm (18-in) trees, 8.9 cm (3.5 in) for 30-cm (12-in) trees, and 10.2 cm (4 in) for 15-cm (6-in) trees *(15)*. Growth in second-growth stands, however, generally exceeds 5.1 cm (2 in) in 10 years for sawlog-size trees *(18)* and a maximum rate in excess of 10.2 cm (4 in) has been reported *(106)*. For the first 30 to 40 years, sugar maples average about 30 cm (12 in) a year in height growth.

Mature trees and stands of sugar maple reach 300 to 400 years of age, 27 to 37 m (90 to 120 ft) in height, and 76- to 91-cm (30- to 36-in) in d.b.h. *(30)*. Following repeated cutting under the uneven-aged system, age and diameter show strong linear relation with the older ages, seldom exceeding 250 years *(68,111)*. Height growth usually ceases or becomes negligible at about 140 to 150 years *(30)*. Diameter growth continues at a decreasing rate with age and size. The largest reported sugar maple tree, growing near Kitzmiller, MD, has a d.b.h. of 209 cm (82.1 in), is 23.8 m (78 ft) tall, and has a crown spread of 20.1 m (66 ft) *(1)*.

Yields of mixed hardwood stands, but predominantly sugar maple, range up to a maximum of 216 m^3/ha (14,000 gross board feet/acre) *(30,70)*.

Yields for northern hardwood stands in the Lake States are available from estimates of average stand age and average stand diameter (table 1). Both parameters are based on overstory trees. Basal-area stocking of stands commonly ranges from 27.6 to 36.8 m^2/ha (120 to 160 ft^2/acre). A few older stands exceed 45.9 m^2/ha (200 ft^2/acre). Even-age and uneven-age silvicultural systems are available for managing stands in which sugar maple is a principal component and a desired species. Periodic annual growth averaging about 4.2 m^3/ha (350 fbm/acre) and annual

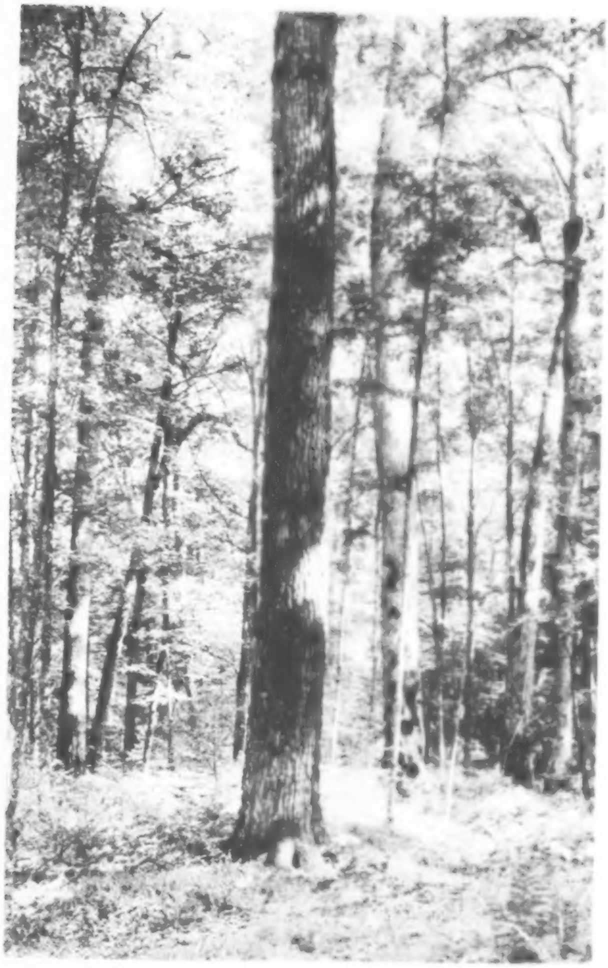

Figure 3—*A mature sugar maple stand in Nicolet National Forest, WI.*

basal-area growth of up to 0.7 m²/ha (3 ft²/acre) is typical of young stands on good sites in the Lake States but varies with total basal-area stocking, distribution of trees by size class, and site *(18)*. Improvement in grade and tree size should be the guiding principle in stand management because this factor contributes more to value increase than diameter growth under most conditions *(41,75,105)*.

Rooting Habit—The root system of sugar maple has strong, oblique laterals with extensive branching. Roots on the upper side of the laterals grow upward into the humus layers and those on the lower side grow downward. Most of the fine feeder roots remain within the general area of origin *(23,103)* Intraspecific root grafting is common.

Although some root growth may continu throughout the year if the soil does not freeze, th bulk of the new root regeneration depends on growt factors exported from physiologically nondorman buds. In northern races of sugar maple, about 2,50

Table 1—Yields from average, well-stocked stands of northern hardwoods in the Lake States dominated by sugar maple (adapted from *29*)

Stand age (yr)[1]	Average d.b.h.	Basal area	Volume	
			Total[2]	Saw lo[3]
	cm	*m²/ha*	*m³/ha*	*m³/ha*
Good site				
40	19	19.7	92.4	13.3
80	29	26.4	193.9	85.4
120	38	31.5	265.3	150.5
160	47	35.6	317.1	197.4
200	56	38.6	350.0	228.2
Medium site				
40	14	18.8	51.8	4.2
80	24	25.0	135.1	49.0
120	31	29.4	202.3	100.8
160	38	32.8	250.6	144.2
200	44	35.6	283.5	176.4
Poor site				
40	10	16.3	25.2	1.4
80	19	22.0	72.1	16.8
120	25	25.9	127.4	53.2
160	30	28.7	175.0	86.1
200	35	30.8	211.4	116.2
	in	*ft²/acre*	*ft³/acre*	*fbm/acre*
Good site				
40	7.4	86	1,320	950
80	11.6	115	2,770	6,100
120	15.1	137	3,790	10,750
160	18.6	155	4,530	14,100
200	22.1	168	5,000	16,300
Medium site				
40	5.6	82	740	300
80	9.5	109	1,930	3,500
120	12.2	128	2,890	7,200
160	14.8	143	3,580	10,300
200	17.4	155	4,050	12,600
Poor site				
40	4.1	71	360	100
80	7.6	96	1,030	1,200
120	10.0	113	1,820	3,800
160	11.9	125	2,500	6,150
200	13.8	134	3,020	8,300

[1] Age determined from overstory trees.

[2] Cubic volumes determined from sound trees 13 cm (5 in) and larger in d.b.h. to a top diameter inside bark of 10 cm (4 in), exclusive of bark.

[3] The Scribner log rule was used for trees 23 cm (9 in) and larger in d.b.h. to a variable top diameter, with a minimum of 20 cm (8 in) inside bark. Deductions were made for cull.

hours of continuous chilling are required to break bud dormancy *(64)*.

Sugar maple roots are extremely sensitive to flooding during the growing season. The roots of maple form both endotrophic and ectotrophic mycorrhizae.

Reaction to Competition—Sugar maple is rated as very tolerant of shade, exceeded among hardwoods only by a few smaller, shorter lived species. In large trees, only American beech *(Fagus grandifolia)* equals it in tolerance under forest conditions *(30)*. Maximum photosynthetic activity generally occurs under about 25 percent of full sunlight. The species can survive for long periods under heavy shade and still show a strong response to release *(30)*.

Release is seldom justifiable for young sugar maple stands subjected to suppression from scattered dominant trees or pin cherry *(Prunus pensylvanica)* because the sugar maple will overcome suppression under those conditions *(30)*. Release is needed, however, when sugar maple competes with striped maple *(Acer pensylvanicum)*, black cherry *(Prunus serotina)*, yellow-poplar *(Liriodendron tulipifera)*, and the oaks *(Quercus* spp.), because growth is retarded and survival is reduced by such competition *(107)*.

One sapling stand study showed that unreleased, dominant trees of good vigor averaged 23 mm (0.9 in) in diameter growth and heavily released trees averaged 46 mm (1.8 in) in diameter growth per year during a 7-year period; unreleased, codominant trees of good vigor averaged 18 mm (0.7 in) in diameter growth and heavily released trees 38 mm (1.5 in). Pole-size trees also respond well to release *(31,102)*.

If released too much, sugar maple readily develops epicormic sprouts from dormant buds *(14,31,33, 36,78)*. Gradual release and good crown development provide adequate control over epicormic sprouting and also enhance natural pruning of epicormic branches on the lower bole. Consequently, proper thinning at scheduled intervals is necessary to encourage quality improvement as well as diameter growth.

Damaging Agents—Early studies in old-growth sugar maple indicated that after two or possibly three cyclic cuts had been made, few damaging agents would affect trees or stands. Current work in second-growth, however, shows some major agents, particularly in even-aged stands *(77,122)*.

At least two species of bud miners, *Proteoteras moffatiana* and *Obrussa ochrefasciella*, overwinter in the terminal bud of sugar maple and kill it. This causes repeated forking, which reduces merchantable log length and adds to the risk of crown loss from splitting. Other bud-damaging insects that may also cause forks are *Choristoneura rosaceana, Cenopis pettitana, Phyllobius oblongus*, and *Platycerus virescens (65,66,77,98,123)*.

Forking at the terminal bud occurs in trees of all ages but is especially pronounced in overstory trees. Side crowding and overhead shading help correct lower forking *(32)*. But early or heavy thinning sets the fork and causes shorter merchantable lengths. As fork members increase in size and weight, fork breakage also increases.

Except for bud losses, sugar maple is not highly susceptible to insect injury and serious outbreaks are not common *(62)*. The most common insects to attack sugar maple are defoliators and these include the gypsy moth *(Lymantria dispar)*, forest tent caterpillar *(Malacosoma disstria)*, linden looper *(Erannis tiliaria)*, fall cankerworm *(Alsophila pometaria)*, spring cankerworm *(Paleacrita vernata)*, greenstriped mapleworm *(Anisota rubicunda)*, Bruce spanworm *(Operophtera bruceata)*, maple leaf-cutter *(Paraclemensia acerifoliella)*, maple trumpet skeletonizer *(Epinotia aceriella)*, and saddled prominent *(Heterocampa guttivitta)*.

One insect of the genus *Phytobia* occasionally causes pith flecks that seriously degrade veneer logs. This insect tunnels the full length of the cambium layer and exits near the root collar *(117)*.

Borers that attack sugar maple include the carpenterworm *(Prionoxystus robiniae)*, sugar maple borer *(Glycobius speciosus)*, maple callus borer *(Synanthedon acerni)*, and occasionally horntails *(Xiphydria abdominalis* and *X. maculata) (95)*.

Sucking insects that affect sugar maple include the woolly alder aphid *(Prociphilus tesselatus)* and other aphid species *(Neoprociphilus aceris* and *Periphyllus lyropictus)* which injure leaves and reduce growth.

Of the scale insects, the maple phenacoccus *(Phenacoccus acericola)*, is the most important to sugar maple. The maple leaf scale *(Pulvinaria acericola)* and the gloomy scale *(Melanaspis tenebricosa)* also frequently attack sugar maple.

Many sugar maple trees died in a small area of Wisconsin and Michigan in 1957 *(113)*. Certain insects—the leaf rollers *(Sparganothis acerivorana* and *Acleris chalybeana)* and the maple webworm *(Tetralopha asperatella)*—combined with disease and climatic factors were thought to be the cause of this mortality *(44,48,61,120)*. The decline has abated but appears to have recurred with less severity on a portion of the same area in the late 1970's.

Diseases of sugar maple generally deform, discolor, or decrease volume but seldom kill the tree *(80)*. The two most important diseases in managed second-growth are probably Eutypella *(Eutypella parasitica)* and Nectria *(Nectria galligena)* cankers. In the Lake States these cankers each affect from about 1 to 4 percent of the trees *(77)* but in Ontario they occur more frequently *(60,87)*. Nectria canker is more prevalent following shelterwood cuttings, probably because conditions favorable for infection are established *(2)*. Two other cankers *(Schizoxylon microsporum* and *Hypoxylon lilakei)* occur rarely on sugar maple. In a few instances cankers may kill a tree but generally only predispose it to breakage.

Some common fungi-causing heart rots in sugar maple are *Armillaria mellea*, primarily a root-rotting fungus; *Hydnum septentrionale*, which causes a soft, spongy, white heart rot; *Inonotus glomeratus*, which causes white to light brown spongy heart rot; and *Ustulina vulgaris*, which causes a butt rot *(30)*.

The amount of defect in sugar maple trees in virgin and unmanaged stands is usually high—commonly from 35 to 50 percent *(30)*. Defect resulting from logging damage usually is minor in small wounds for as long as 10 years, but 20-cm (8-in) scars all were infected within 20 years and value losses were significant *(47,81)*.

Logging injuries to the stems of residual trees and to reproduction frequently result in the entrance of decay and eventually serious volume loss *(6,79)*. In a study in Upper Michigan at least 30 percent of the logging scars on the main stem of older trees resulted in serious defects within 15 to 20 years *(30)*. Larger limbs broken in logging also usually result in serious defects *(93,94)*. In Upper Michigan after a 20-year period about 8 percent cull resulted from decay and stain that had entered through scars on limbs 10 cm (4 in) and larger *(30)*. Smaller limb breakage exposing only sapwood, however, generally results in little volume loss *(4,30)*.

Two wilts occasionally attack and kill sugar maple. Sapstreak, caused by *Ceratocystis coerulenscens*, enters through root injuries from logging and has been reported in several localities *(56,57,80)*. Verticillium wilt, caused by *Verticillium albo-atrum*, is usually found only in shade trees. This wilt also invades the trees through the roots.

When stored for more than a year, a saprophytic fungus, *Cryptostroma corticale*, sometimes develops on the bark of sugar maple. The spores from this fungus are released during processing and have caused bronchial asthma and severe allergenic lung disorders to millworkers *(83,84)*.

Physical and climatic injuries often occur on sugar maple. Much damage from glaze storms occurred in New York in 1942. The injured trees showed a slight tendency to sprout and renew growth. Many of the smaller trees that had 85 percent or more of their crown broken away developed saprot *(30)*.

Winter sunscald frequently occurs in even-aged sugar maple stands. Trees are damaged from late winter heating of the bole above the snowline on bright sunny days followed by rapid freezing that ruptures the cells. Most injury occurs when the stems are 2.5 to 7.6 cm (1 to 3 in) in d.b.h., and certain topographic positions are affected more than others (55). Healing in dense stands is slow, if at all, and later stages often appear to be a simple frost crack. Various fungi may be present but may or may not prevent closure *(59)*. Part of the lack of closure may be due to shrinkage and swelling of the bole associated with changes in air temperature *(35)*.

In some areas the lower portion of sugar maple boles contains many vertical cracks from 2.5 to 7.6 cm (1 to 3 in) long. Although these cracks have been termed annual maple cankers, the causal agent does not seem to be a fungus. These cankers slowly disappear and new ones recur at short intervals *(32)*. In Pennsylvania they were most common on slowly permeable soils *(116)* but no specific cause has been identified *(3,58)*.

Sugar maple can be severely damaged from deicing road salt *(96)*. In an industrial area the number of overstory sugar maples was markedly reduced from exposure to sulfur oxides, nitrogen oxides, chlorides, and fluorides. Sugar maple remained an abundant species in the understory because of a lower exposure level *(72)*.

Numerous animals feed on or injure sugar maple without serious effect except in local and limited situations. Deer browsing is probably the most common wildlife factor. Winter browsing in the Lake States causes little damage or reduced growth *(51,100)*. In the central Adirondacks, however, continual browsing of sugar maple allows American beech, which the deer avoid, to dominate northern hardwood understories *(54)*.

Red, grey, and flying squirrels sometimes gnaw or feed on the seed, buds, foliage, and twigs of sugar maple. In rare instances, they have girdled and killed larger branches and tree tops *(30,100)*. Porcupines may feed on the bark and kill the top by girdling the upper stem *(8,30)*.

Sapsuckers frequently peck and cause degrade in some sugar maple trees but rarely, if ever, kill the tree *(19,82,90,92)*. On heavily pecked trees in the spring a fungus develops on the sap and causes the bark to turn black *(82)*. Such trees probably should be retained in the stand to prevent other trees from being attacked.

Special Uses

The sugar maple tree is the principal source of maple sugar. The trees are tapped early in the spring for the first flow of sap, which usually has the highest sugar content. The sap is collected and boiled or evaporated to a syrup. Further concentration by evaporation produces the maple sugar. Sugar maple sap averages about 2.5 percent sugar; about 129 liters (34 gal) of sap are required to make 3.8 liters (1 gal) of syrup or 3.6 kg (8 lb) of sugar. Guides have been printed for developing a sugar bush from natural stands *(67)*.

Breeding experiments have determined that sugar content is high for certain families and that sugar content in individual trees is consistent over a period of years *(64,104)*. A sugar content of 7.4 percent has been attained by crossing two selected parents of slightly lower content *(64)*. The sugar content is also correlated with the volume yield of sap *(7,74)*.

Genetics

Sugar maple is a genetically variable tree. Some botanists recognize from three to six varieties or forma that differ in morphological characteristics, but others consider them to be subspecies. Extensive research indicates a "flow of characteristics" over the wide geographic distribution and variation in habitat conditions *(30,64)*. Kriebel indicated that sugar maples could be grouped into three major geographic races or ecotypes, each containing a parallel clinal variation *(30)*. Provenance tests in his study indicate differences in drought endurance, resistance to leaf injury from high insolation, and phenological behavior.

Most of the genetic work in sugar maple is currently confined to improving maple syrup *(27)* and developing ornamental trees *(49,62,119)*. Nurserymen rely mostly on budding and some grafting for vegetative propagation. Bird's-eye grain trees have been grafted since the early 1960's but results are not available for propagation of this characteristic *(63)*. The USDA Forest Service, in recent work, has selected 228 superior sugar maple trees and established three plantations with 126 families *(43)*.

Hyrbids have been reported between sugar maple and black and red maples *(30)*. Hybrid seedlings have been obtained by pollinating sugar maple with another maple (presumably *Acer macrophyllum*) *(30)*.

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Aesculus glabra Willd. Ohio Buckeye

Hippocastanaceae Horsechestnut family

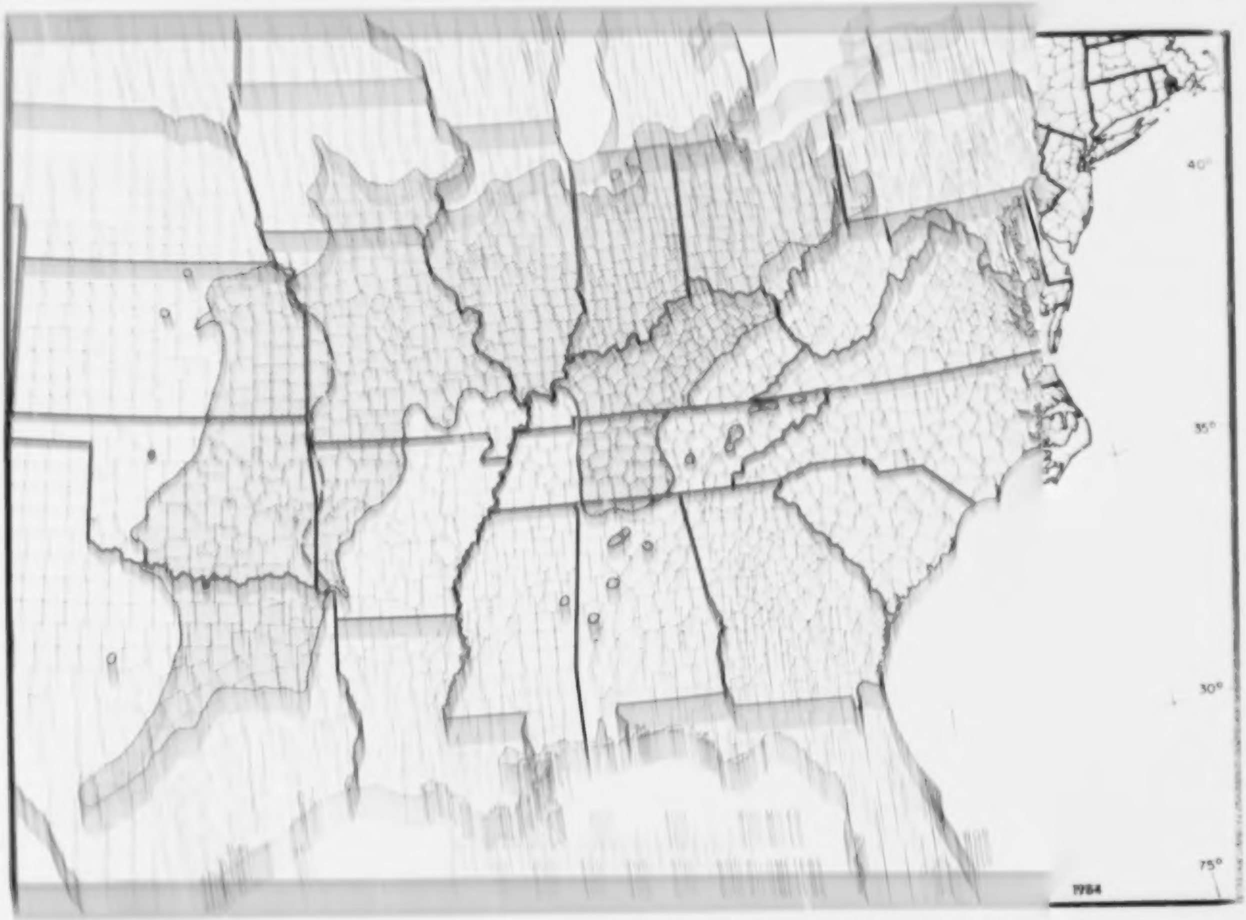
Robert D. Williams

[illegible]

Habitat

Native Range

[illegible] stly on mesophytic [illegible] hio, and southern [illegible] ral Iowa. Its range [illegible] southwestern O [illegible] western Arkansas,



[illegible] variety arguta, Texa

[illegible]

Tennessee, and central Alabama with one location in eastern Mississippi *(9)*. It has been planted in Europe and the eastern United States; in eastern Massachusetts, Minnesota, and western Kansas *(11)*.

Climate

The average annual temperature in the growing area of Ohio buckeye ranges from about 4° to 10° C (40° to 50° F) *(6)*. Average minimum temperatures are not below −29° C (−20° F) within its range, but −40° C (−40° F) temperatures have been recorded where it grows in Missouri and Iowa. Maximum temperatures as high as 46° C (115° F) have occurred in the western part of its range. Average annual precipitation ranges from 760 mm (30 in) in Kansas and Oklahoma to 1020 mm (40 in) in Ohio and western Pennsylvania, and up to 1400 mm (55 in) in Mississippi and Alabama. Growing-season precipitation averages 510 to 640 mm (20 to 25 in). Snowfall ranges from 5 cm (2 in) in the southern part of the geographic distribution to 102 cm (40 in) in the northern part. About 160 days are frost-free in the northern part of the range and as many as 220 days in the southern part.

Soils and Topography

The buckeye is a moist-site tree and is most frequently found along river bottoms and in streambank soils. It is often found on the moist soils of the Early Wisconsin Drift Plain in Indiana *(4)*. Ohio buckeye is most commonly found growing on soils of the order Alfisols. In the early 1800's buckeye and sugar maple (*Acer saccharum*) were prominent on the slope phase of the Miami silty clay loam in Ohio *(9)*. Buckeye made up about 5 percent of the forest stand on this soil type. Since then its abundance has diminished.

Although Ohio buckeye is sometimes found on drier sites such as those supporting oak-hickory stands, and on clayey soils, it usually grows slowly in these situations and seldom becomes dominant. It is a shrub, only 1.2 to 1.5 m (4 to 5 ft) tall, on dry habitats in the oak-hickory association of eastern Oklahoma *(9)*. Ohio buckeye also is found in hardwood stands on moist sites in the limestone-sink-and-cave section of the Bluegrass region of Kentucky and is infrequently found on the well developed flood plains along the Missouri River in southeastern Nebraska *(9)*.

Associated Forest Cover

Ohio buckeye grows in mixed stands with bur oak (*Quercus macrocarpa*), chinkapin oak (*Q. muehlenbergii*), white ash (*Fraxinus americana*), hackberry (*Celtis occidentalis*), sugar maple, black walnut (*Juglans nigra*), black cherry (*Prunus serotina*), honeylocust (*Gleditsia triancanthos*), Kentucky coffeetree (*Gymnocladus dioicus*), shagbark hickory (*Carya ovata*), American elm (*Ulmus americana*), and red mulberry (*Morus rubra*) in the Bluegrass region of Kentucky *(9)*. In Indiana, 6 percent of the trees in a mixed hardwood stand were buckeyes; 39, 11, 16, and 28 percent were sugar maple, American elm, black walnut, and miscellaneous species, respectively. In another stand in which more than 50 percent of the trees were beech (*Fagus grandifolia*), sugar maple, hackberry, and black walnut, buckeye constituted a little more than 10 percent.

In the mixed mesophytic climax forests of Marion and Johnston Counties, IN, in 1819, Ohio buckeye made up 6 and 2 percent, respectively, of the total number of stems *(9)*, and less than 2 percent of these trees were more than 46 cm (18 in) in d.b.h. In a few stands, however, it made up as much as 17 percent of the total stems, ranking second in importance only to beech.

Buckeye is a frequent or even a common tree in association with beech, sugar maple, and American basswood (*Tilia americana*) in the Wabash River Basin in southern Illinois and Indiana *(9)*.

Ohio buckeye is not listed by the Society of American Foresters as a major or minor component of any of the North American forest cover types *(5)*, probably because of its relatively minor commercial importance and its increasing rarity. It is not a pioneer tree and thus is seldom found on old fields or spoil-bank sites.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Ohio buckeye is polygamo-monoecious, bearing both bisexual and male flowers. The pale greenish-yellow flowers appear after the leaves in the spring from March to May and are borne in upright branched clusters. Only those near the base of the branches of a cluster are perfect and fertile; the others are staminate *(4,11)*. The fruit is a leathery capsule containing one, two, or three seeds. The ripe seed is dark chocolate to chestnut brown, smooth and shiny, with a large, light-colored hilum so that it resembles an eye. The cotyledons are very thick and fleshy and contain no endosperm.

Seed Production and Dissemination—Seeds are dispersed from early September to late October by gravity, by animal activity, and sometimes by water. The number of hulled seeds per kilogram ranges from 105 to 150 (48 to 67/lb), and most seeds are sound *(11)*. The seeds have a high moisture content and should be kept moist to avoid loss of viability.

Ohio buckeye begins bearing seeds at 8 years but no data are available on frequency and amount of seed produced *(11)*.

Seedling Development—The seeds ordinarily germinate in the spring after wintering on the ground. Germination is hypogeal. If seeds are to be sown in a nursery, they should be sown in the fall or stratified about 120 days before spring sowing *(11)*. No germination has been observed on dry surface soil, even with an ample seed supply.

Seedlings can grow under some shade, but the species seems to develop best as isolated individuals in openings along streambanks and on other moist sites. No data are available on early growth rates.

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—Ohio buckeye generally develops a strong taproot the first year. Most of the shoot growth occurs early in the growing season. As a sapling it grows faster than most of the oaks but slower than yellow-poplar *(Liriodendron tulipifera)*. In the open, it is characteristically branchy with a short, knotty trunk.

Fifty Ohio buckeyes measured in Jefferson County, IN, averaged 20.7 m (68 ft) in height and 84 cm (33 in) in d.b.h., 91 cm (36 in) above the ground *(9)*. Apparently these trees were larger in diameter than average for buckeye, even though the diameter was measured lower on the bole than the standard breast height of 1.37 m (4.5 ft). This species generally does not grow taller than 9.1 m (30 ft) and seldom exceeds 21.3 m (70 ft) *(9)*. In 1978, the largest living tree registered was 116 cm (45.5 in) in d.b.h., 44.5 m (146 ft) tall, and had a crown spread of 16.5 m (54 ft) *(1)*. Trees larger than 61 cm (24 in) in diameter are rare. On good sites, the tree will reach usable sawtimber size at 60 to 80 years of age. On poor sites, it seldom has the form or size to produce saw logs.

Rooting Habit—No information available.

Reaction to Competition—Because Ohio buckeye is often found in beech-sugar maple stands, it must be classed as shade tolerant. It only attains good form as a timber tree when it grows in reasonably dense stands. Side competition and shade foster straight boles and encourage natural pruning of this tree, which tends to have a large, branchy crown.

Damaging Agents—Ohio buckeye is relatively free of insect pests but the sapwood timberworm *(Hylecoetus lugubris)*, the lacebug *(Corythucha aesculi)*, the chrysomelid *(Derocrepis aesculi)*, and the walnut scale *(Quadraspidiotus juglansregiae)* feed on buckeye *(2)*.

Ohio buckeye also has relatively few diseases *(7)*. It is susceptible to a leaf blotch *(Guignardia aesculi)*, which begins as brown spots or blotches on the leaves and may eventually involve all the leaves, giving the tree a scorched appearance. This disease may slow the growth rate but does no permanent damage to the tree and can be controlled on ornamentals. One of the powdery mildews, *Uncinula flexuosa*, also attacks the leaves of buckeye.

A leaf rust of the Ohio buckeye that occurs in the western part of the species range was long known as *Aecidium aesculi* but has now been established by Baxter as *Puccinia andropogonis (3)*.

Leaf blotch and leaf scorch, the latter involving a physiogenic response to heat and drought along urban streets, may be the most serious diseases *(7)*. Air pollution may be more responsible for the leaf blighting than heat or drought.

Because Ohio buckeye leafs out early in the spring, the young leaves are sometimes killed by frost. This species is capable of withstanding severe winters, however, and has been successfully introduced in Minnesota and Massachusetts. Moreover, the bole of the tree is not commonly damaged by frost, and the heavy branches of the crown are seldom severely damaged by heavy loads of sleet or snow. Apparently buckeye is not susceptible to sunscald either.

The common eastern leafy mistletoe, *Phoradendron serotinum*, occurs on Ohio buckeye, but damage is negligible *(7)*.

Fungi capable of causing either rot of the central stem or rot at wounds of living trees include *Ganoderma applanatum, Oxyporus populinus, Phellinus johnsonianus,* and *Polyporus squamosus (7)*. Buckeye growing in forest stands is usually free of defect caused by decay unless the bole has been damaged by fire.

Special Uses

The seeds as well as the bark of Ohio buckeye are reported to be poisonous, and the *Aesculus* native to Illinois is known to contain a poisonous narcotic glucoside *(9)*. The young shoots of buckeye are poisonous to cattle, and landowners in Indiana have exterminated buckeye in many areas because the seed is considered poisonous to livestock *(9)*. On the other hand, some buckeye seed are apparently eaten by squirrels. In Ohio, it constitutes from 2 to 5 percent of the food of eastern fox squirrels during the fall, winter, and spring seasons. Other studies in Ohio list buckeye as an auxiliary food that was sampled by squirrels in September but not eaten in quantity *(9)*. Thus, it seems probable that the use of buckeye seed for food by animals is not a limiting factor in its reproduction.

Fox squirrels in Illinois were observed eating the pith from terminal twigs *(6)*. Buckeye pith contains 60 percent raffinose, a sweet-tasting 18-carbon sugar that is much sweeter and contains potentially more energy than sucrose.

The wood is light and soft and is used for pulpwood, woodenware, and occasionally for lumber *(10)*.

Genetics

Texas buckeye *(Aesculus glabra* var. *arguta* (Buckl.) Robins.), a shrub or small tree, ranges from southeastern Nebraska southwest to central Texas *(8)*.

Hybrids of *Aesculus glabra* with *Ae. octandra* (*Ae.* × *marylandica* Booth ex Dippel), *Ae. pavia* (*Ae.* × *bushii* Schneid.), and *Ae. octandra* × *pavia* (*Ae.* × *arnoldiana* Sarg.) have been recorded *(8)*. Intermediate hybrids exhibiting the characteristics of both species occur as hybrid swarms, or most often, individual plants of one species have one or more characteristics of the other species from introgression *(4)*.

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Aesculus octandra Marsh. Yellow Buckeye

Hippocastanaceae Horsechestnut family

Robert D. Williams

Yellow buckeye (*Aesculus octandra*), also called sweet buckeye or big buckeye, is the largest of the buckeyes and is most abundant in the Great Smoky Mountains of southeastern United States. It grows best on moist and deep, dark humus soils with good drainage in river bottoms, coves, and northern slopes. The young shoots and seeds contain a poisonous glucoside that is harmful to animals, but the shape and foliage make this an attractive shade tree. The wood is the softest of all American hardwoods and makes poor lumber, but it is used for pulpwood and woodenware.

Habitat

Native Range

The range of yellow buckeye (figs. 1, 2) extends west from the mountains of southwestern Pennsylvania down the Ohio River Valley to extreme

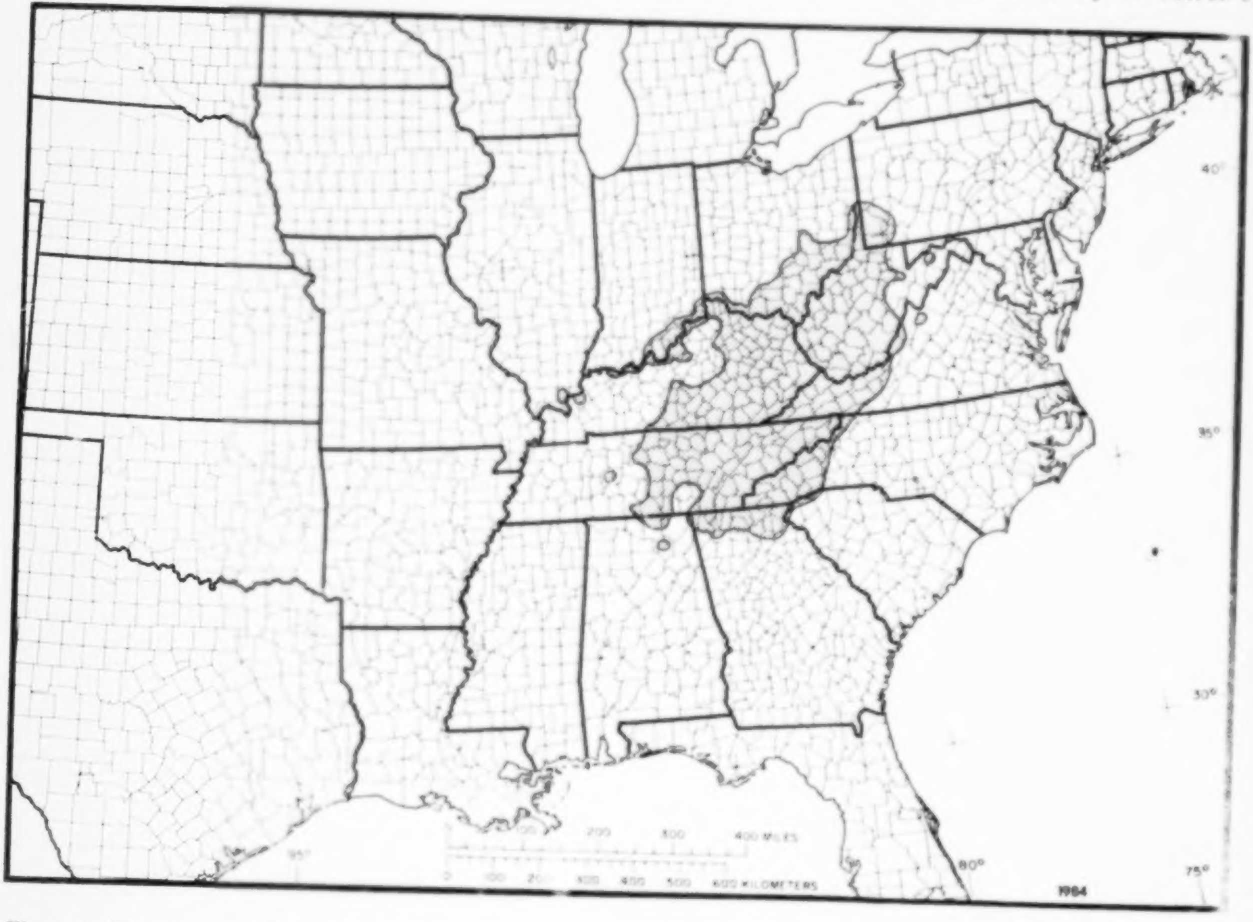

Figure 1—*The native range of yellow buckeye.*

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Figure 2—*A yellow buckeye among cove hardwoods in North Carolina.*

southeastern Illinois; south to Kentucky, central Tennessee, and northern Alabama; east to northern Georgia and extreme northwestern South Carolina; and north to western Virginia and West Virginia *(7)*.

Climate

Yellow buckeye grows in a wide variety of climates. Average annual precipitation ranges from 2130 mm (84 in) per year in local mountainous areas of western North Carolina to 990 mm (39 in) in southern Ohio, Indiana, and Illinois. The average annual snowfall ranges from 102 cm (40 in) in the mountains to less than 13 cm (5 in) in the southern part of the range. Average annual temperature is 10° C (50° F) in southwestern Pennsylvania and 16° C (60° F) in northern Georgia; average annual minimum temperatures are no lower than -18° C (0° F), and average annual maximum temperatures do not exceed 38° C (100° F). The frost-free period ranges from 150 days in the mountains of West Virginia to 210 days in northern Alabama and Georgia.

Distribution within the State of Ohio is influenced by climate which may be modified by topography *(3)*.

Soils and Topography

Yellow buckeye grows best in river bottoms, along stream banks, and in the deep soils of the North Carolina and Tennessee mountains *(4)*, generally on soils of the orders Alfisols and Entisols. It is a bottom-land tree in the northern part of its range, but farther south it grows on high mountainous slopes. It attains its largest size and is most numerous in coves and on northern slopes in the mesophytic forests of the Appalachian and Cumberland Mountains, and it usually is found on deep dark soils with a crumb, mull humus. Yellow buckeye is a more mesophytic tree than Ohio buckeye (*Aesculus glabra*) *(4)*.

Yellow buckeye is abundant in the mesophytic forests almost to the boundary of Wisconsin glaciation *(4)*. It grows locally within the area of Illinoian glaciation in Ohio and Indiana but is seldom found within the area of Wisconsin glaciation.

Buckeye is considered a climax tree whose northward range was abruptly reduced during Pleistocene glaciation. If this is true, a reextension of its range northward probably has not occurred because the present environment is unfavorable *(4)*.

The greatest concentration of yellow buckeye in the Great Smoky Mountains of North Carolina and Tennessee is in mesic coves, canyons, and ravines. The tree is commonly found at elevations from 460 to 1860 m (1,500 to 6,100 ft), with the greatest numbers occurring between 1220 and 1520 m (4,000 and 5,000 ft) *(4)*.

In the higher Cumberland Mountains extending from about 460 or 610 m (1,500 or 2,000 ft) in elevation upward for about 300 m (1,000 ft), yellow buckeye may make up from 15 to 30 percent of the canopy trees in the sugar maple–basswood–buckeye forest. West of the Appalachians and in the Central States, it is found locally and is usually confined to mesophytic sites in coves, ravines, and bottoms.

Associated Forest Cover

The mixed mesophytic forests in the southern Appalachian Mountains and in the Cumberland Plateau Region include many species of trees, and yellow buckeye is usually a constant member of these associations. It composes 15 to 23 percent of the upper canopy trees in the stands studied in that region.

Yellow buckeye is a common associate in the Sugar Maple (Society of American Foresters Type 27) forest cover type of the central hardwood zone and the Appalachian highlands *(5)*. It is a minor associate in five other types: Red Spruce–Yellow Birch (Type 30) and Red Spruce (Type 32) in the southern Appalachians, Red Spruce–Fraser Fir (Type 34) at the lower altitudinal range of this type, Northern Red Oak (Type 55) on moist sites in the eastern part of the type range, and Yellow-Poplar–White Oak–Northern Red Oak (Type 59) at higher elevations.

The soil and topographic conditions that are good for yellow buckeye growth generally are also excellent for the growth of yellow-poplar *(Liriodendron tulipifera)*, white ash *(Fraxinus americana)*, and various oaks *(Quercus* spp.*)*. Many of the herbaceous plants that indicate excellent oak sites in West Virginia are probably indicative of equally good sites for yellow buckeye *(4)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yellow buckeye is polygamo-monoecious; the yellow or yellowish-white flowers on a single inflorescense may be either staminate or perfect. They appear from April to June after the leaves. Only those flowers near the base of the branches of an inflorescence are perfect and fertile. The others are staminate and infertile.

The fruit of yellow buckeye is a rounded leathery three-parted capsule, 5 to 8 cm (2 to 3 in) long. More than half of the capsules are one-seeded, although two-, three-, and four-seeded forms are found in decreasing frequencies. The fruit of buckeye is potentially six-seeded, so variation in seed number may be due to aborted ovules caused by incomplete fertilization *(4)*. The ripe seed is dark chocolate to chestnut brown, smooth and shiny, with a large light-colored hilum so that it resembles an eye. The cotyledons are very thick and fleshy and contain no endosperm.

The seeds ripen and are dispersed in September by gravity, animal activity, and sometimes water. Number of cleaned seed per kilogram ranges from 60 to 66 (27 to 30/lb). Almost all seeds are sound. Following collection, the seeds should be kept moist to avoid loss in viability. Seeds require about 120 days stratification or prechilling to induce prompt germination *(8)*. Germination usually is complete 3 to 4 weeks after spring sowing.

Seed Production and Dissemination—No information is available as to the age at which yellow buckeye trees begin bearing seeds, the number of seeds produced by individual trees, the conditions favoring seed production, or the frequency of seed years.

Seedling Development—Germination is hypogeal. It occurs in early spring after the seeds have wintered on the ground. Yellow buckeye develops a large taproot following germination. No reports are available concerning germination and early growth and survival of yellow buckeye under natural conditions. The natural occurrence of the tree indicates that moist, deep soils are most favorable for the germination of seeds and survival of seedlings.

Vegetative Reproduction—The sprouting ability of yellow buckeye is not known. As in most hardwoods, however, sprouting is probably more vigorous when trees are cut at a young age. Trees that have apparently originated from sprouts have been observed in southeastern Ohio.

Sapling and Pole Stages to Maturity

Growth and Yield—Yellow buckeye, like Ohio buckeye, is one of the first trees to leaf out and begin shoot growth in the spring. General observation indicates that it has an intermediate growth rate. Under forest conditions it attains large size, has a long clean trunk, and is the largest of all native buckeyes. A large tree found in the Smoky Mountains National Park had a d.b.h. of 155 cm (61 in), a height of 26 m (85 ft), and a crown spread of 16.5 m (54 ft) *(4)*. The American Forestry Association's National Register of Big Trees in 1982 recorded the largest known living specimen, located near Bowers Creek, KY, as having a d.b.h. of 124 cm (49 in), a height of 42.7 m (140 ft), and a crown spread of 16.5 m (54 ft) *(1)*. Yellow buckeye is probably long lived. It reaches relatively large size and maintains itself in the mixed mesophytic forest.

Rooting Habit—No information available.

Reaction to Competition—Yellow buckeye becomes established, survives, and grows in competition with its associates of the mixed mesophytic forest; thus, it must be classed as a shade-tolerant tree. The local occurrence and small number of yellow buckeye probably is due to limited seed dissemination and to the inability of the tree to establish itself on any but the most favorable sites. The critical period of competition for this species appears to be during germination and in the early life of the seedling.

Yellow buckeye is not a pioneer species and is seldom found on old fields or on other open land. The loss of viability in seed exposed to drying limits germination on dry, exposed sites.

Damaging Agents—No major insect enemies of yellow buckeye are known that consistently cause severe defoliation or damage to the woody parts of the tree. A buckeye lacebug *(Corythucha aesculi)* has been reported as a defoliator of buckeyes, and in southeastern Ohio the yellow buckeye frequently is infested by this insect *(2,4)*. The insect damages the leaves during ovipositing, stomata are blocked by multitudinous flecks of fecal matter, and nymphs feed on the leaves. Foliage on the young trees and on the lower branches of older trees is attacked early in the spring, because yellow buckeye is one of the first trees in southeastern Ohio to leaf out. By the middle of July, leaves turn yellowish or brown and many young trees are nearly defoliated. This injury does not kill the trees, but it probably retards growth. The sapwood timberworm *(Hylecoetus lugubris)* tunnels under the bark and across the sapwood and causes pinhole defects. *Derocrepis aesculi* feed on buckeye leaves *(2)*. Yellow buckeye is occasionally attacked by the walnut scale *(Quadraspidiotus juglansregiae) (2)*.

Yellow buckeye is relatively free of diseases. Leaf blotch, *Guignardia aesculi*, is the most destructive disease affecting the buckeyes and horsechestnut. Rainy seasons are especially favorable for the germination of the spores of this disease. When trees are severely affected, from a distance the foliage appears to have been scorched by fire, and the disease may cause much defoliation.

A powdery mildew, *Uncinula flexuosa*, attacks the leaves of buckeye, and a leaf spot *Cercospora aesculina*, and other localized diseases of buckeye have been reported *(4)*. A leaf scorch that first develops near the leaf center and extends outward mainly between the veins commonly appears on urban street trees and has been attributed to heat and drought; but air pollution should also be suspect *(6)*.

Yellow buckeye wood is relatively free from fungus defects. Only *Polyporus squamosus (9)* and *Collybia velutipes (4)* have been reported associated with rot in living trees, although other rot fungi probably attack dead wood.

Special Uses

The abundant, large nuts of yellow buckeye contain much starch but are apparently not suitable for food because they contain a poisonous glucoside, aesculin. The American Indian ate yellow buckeye nuts but first they roasted the nuts among hot stones and then peeled and mashed them and leached them with water for several days. This treatment apparently removed the aesculin.

Young shoots and seeds of buckeye have also been reported to be poisonous to livestock *(4)* and some landowners in Indiana have eradicted buckeye for this reason. Because the seeds of yellow buckeye are poisonous, wild animals do not use them for food and therefore animals probably do not limit the reproduction of this species. The wood is used for pulpwood, woodenware, and sometimes for lumber.

Genetics

The buckeye frequently have chromosome irregularity and pollen is often sterile *(4)*. This has been considered as evidence of hybridization among the various buckeyes. One report indicated that in glaciated areas where *Aesculus octandra* is not found, its germ plasm has infiltrated the populations of *A. glabra (4)*. *A. octandra* and *A. glabra* do hybridize, and intermediates showing the characters of both species occur as hybrid swarms. More often, individual plants of one species have one or more characters from introgression with the other species *(3)*.

Yellow buckeye hybridizes with *Aesculus glabra* (*Ae.* × *marylandica* Booth ex Dippel); *Ae. sylvatica* (*Ae.* × *neglecta* Lindl., *Ae.* × *glaucescens* Sarg.); *Ae. pavia* × *sylvatica* (*Ae.* × *woerlitzensis* Koehne, *Ae.* × *dupontii*, Sarg.) *(7)*.

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Ailanthus altissima (Mill.) Swingle **Ailanthus**

Simaroubaceae **Quassia family**

James H. Miller

Ailanthus (*Ailanthus altissima*), also called tree-of-heaven, Chinese sumac, paradise-tree, and copal-tree (fig. 1), is an introduced species that has become widely naturalized across the continent. Ailanthus has found an extremely wide variety of places to establish itself, from urban areas to reclaimed surface mined lands. Its successful reproduction on impoverished soils and in harsh environments results from its ability to sprout from the roots and to seed prolifically. Ailanthus is found as an upper-canopy component, with varying frequency, in the eastern hardwood forests, apparently spreading by sprouting after harvest disturbance.

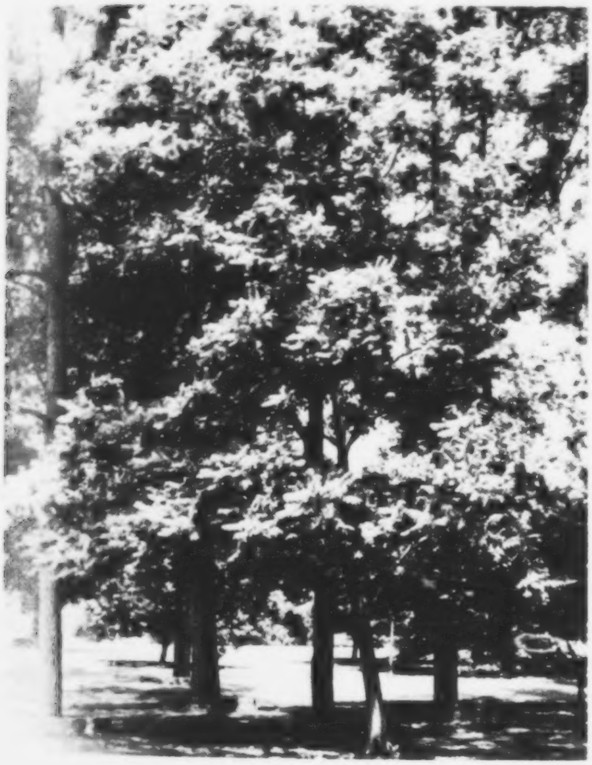

Figure 1—*Ailanthus*.

Habitat

Native Range

Ailanthus, a native of China, was first introduced into the United States from England to Philadelphia, PA, in 1784. Extensive plantings in cities during the 1800's has resulted in its naturalization across the United States. An eastern range extends from Massachusetts, west to southern Ontario, southwest to Iowa, south to Texas, and east to northern Florida. It is found in less abundance from New Mexico west to California and north to Washington.

Climate

Because of its wide distribution, ailanthus grows under a variety of climatic conditions. Within the naturalized range of the species, the climate can be temperate to subtropical and humid to arid. In arid regions bordering the Great Plains, low precipitation, from 360 to 610 mm (14 to 24 in) annually with 8 dry months, can be tolerated (*7*), whereas in humid localities in the southern Appalachians rainfall can exceed 2290 mm (90 in) annually (*15*). Annual maximum and minimum temperatures are -9° and 36° C (15° and 97° F). Extreme cold and prolonged snow cover restricts the elevational range to the lower slopes of the Rocky Mountains and prolonged cold temperatures have reportedly caused dieback, but resprouting occurs (*1,7*).

Soils and Topography

Ailanthus grows best in loamy, moist soils but tolerates a wide range of textures, stoniness, and pH. On the dry end of the moisture spectrum it is drought hardy, and on the wet end it cannot tolerate flooding. The species is widely recognized by the urban populace since it frequently occupies and covers untended areas in cities. The species' tolerance of harsh sites led to testing for strip mine reclamation; a study in eastern Kentucky found ailanthus better adapted to acid spoil than to calcareous spoil and capable of growing on spoils with low to moderate phosphorus (*17*). Soils on which ailanthus is most commonly found are within the orders Ultisols, Inceptisols, and Entisols.

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Associated Forest Cover

Because of ailanthus' scattered and disjunct occurrence over a wide geographical range, a listing of associated species would have little significance. Forest stands around cities are common areas of invasion and establishment, but it may be an occasional or minor component of forests following disturbance anywhere within its naturalized range.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The yellowish-green flowers of ailanthus appear from mid-April to July, south to north, depending on latitude. The flowers are arranged in large panicles at the ends of new shoots. A dioecious species, it bears male and female flowers on different trees, with male trees producing three to four times more flowers than are usually found on female trees *(11)*. Male flowers are more conspicuous than female ones, emitting a disagreeable odor that attracts numerous insects. The foul odor of the male flowers makes the tree less favored for ornamental plantings in cities.

Seed Production and Dissemination—Pollination occurs in the spring and clusters of seed ripen from September to October. The fruit is a samara with the seed in the center of a thin, oblong wing, well adapted for wind dispersal. The ripe samaras are greenish yellow or reddish brown. The seed usually persists on the female tree through the winter, characterizing their appearance, but can be dispersed any time from October to the following spring. The species is a prolific seeder; the most abundant seed production is from trees that are 12 to 20 years.

After collection, seeds should be spread to air-dry. Number of seeds per kilogram averages from 27,000 to 33,000 (12,235 to 14,970/lb) and germination after cold stratification averages 65 to 85 percent *(7,18)*. Seeds should be stored dry in sealed containers. The recommended cold stratification is 5° C (41° F) in moist sand for 60 days.

Seedling Development—Seeds can be sown immediately upon ripening or stratified until spring. In nurseries, seeds are usually sown in the spring and seedlings transplanted early the following spring. Germination is epigeal. Vigorous first-year seedling growth of 1 to 2 m (3.3 to 6.6 ft) has been reported *(1,11)*. Average survival on 11 different plantings in Indiana strip mines was 74 percent after the first growing season and then decreased to 58 percent after the first winter *(5)*. This illustrates the winter damage and mortality frequently reported *(1,7)*.

Because ailanthus is intolerant of shade, reproduction in natural stands appears sparse and erratic except by sprouting.

Vegetative Reproduction—The dense thickets of ailanthus reproduction on disturbed soils of road cuts and city building sites develop from root sprouts. Prolific root and stump sprouting has discouraged use of ailanthus as an ornamental species. After death or injury of the main stem the wide-spreading shallow root system can give rise to an abundance of sprouts. Sprouts have shown first-year height growth of 3 to 4 m (10 to 13 ft) *(19)*. Thus, the species can be easily propagated from either root cuttings or from coppicing.

Sapling and Pole Stages to Maturity

Growth and Yield—Information on the growth and yield of ailanthus in the United States at this time is lacking. Maximum heights are often reported as 17 to 27 m (56 to 90 ft) and a maximum d.b.h. as 100 cm (40 in) *(10,12)*. A short-lived species, it lives 30 to 50 years *(20)*. On arid sites, 15 m (50 ft) or more of height growth can be reached in 25 years, with a straight bole for 10 to 12 m (33 to 40 ft) *(7)*. At a New England location, trees reached a 10 to 15 m (33 to 49 ft) height and 9 to 11 cm (3.7 to 4.3 in) d.b.h. in 30 years *(11)*.

Rooting Habit—Ailanthus roots are shallow spreading, often apparent at the soil surface, and roots near the trunk thicken into enlarged storage structures. These large rounded structures are assumed to be for water storage, contributing to the drought hardiness of the species *(4)*. There is a general absence of a taproot with most roots present in the upper 46 cm (18 in) of soil. Within this zone, the deeper roots send numerous small roots to the surface. Adventitious shoots may arise from any of the surface roots.

Reaction to Competition—Ailanthus is a successional pioneer species, intolerant of shade *(8)*. I competes successfully in mixed stands of hardwood throughout its range, indicating that it was presen at the start of stand establishment.

Allelopathic effects on over 35 species o hardwoods and 34 species of conifers have bee demonstrated for water extracts of ailanthus leave *(14)*. Only white ash *(Fraxinus americana)* was n adversely affected. Germination and growth of slas and Monterey pines (*Pinus elliottii* and *P. radiata*) were inhibited by scattering leaves of ailanthus collected in June and July on the seed bed surface, while leaves collected in October stimulated germination and growth *(22)*. Such studies point to a strong allelopathic role for ailanthus in forest succession.

Damaging Agents—The species is relatively resistant to insect predation *(7)*. Three insect species are known to feed on ailanthus foliage, however *(2)*. Most noted of the foliage feeders in the eastern range, especially in the South, is the ailanthus webworm (*Atteva punctella*). Larvae from this insect feed on leaves enclosed in a frail, silken web. Another larval feeder, imported from Asia, is the cynthia moth (*Samia cynthia*). Ailanthus is the preferred host for this insect, but wild cherry and plum can also become infested. The Asiatic garden beetle (*Maladera castanea*) feeds on numerous plants during night flights, including ailanthus.

Although many fungi have been reported on the leaves and twigs of ailanthus, the tree suffers little from disease, and its pathology need rarely be a consideration in its culture *(9)*. If ailanthus can be said to be subject to a major disease it would be Verticillium wilt (*Verticillium albo-atrum*). Many trees were killed by this soil-borne wilt in Philadelphia in 1936. Shoestring root rot (*Armillaria mellea*) has been reported in trees in New York *(16)*.

While this tree is rated moderately susceptible to Phymatotrichum root rot (*Phymatotrichum omnivorum*) in Texas, it is considered most satisfactory for planting in the southern parts of Texas root rot belt *(20,23)*.

In Texas, seeds are eaten by a number of birds, including the pine grosbeak and the crossbill *(21)*. Occasional browsing by deer has also been reported.

Wind, snow, and hard freezes are damaging to tops of seedlings, while mature trees are resistant to ice breakage *(3)*. Resprouting usually occurs, although repeated damage leads to a reduction in seedling survival.

Special Uses

Ailanthus's main importance remains in urban forestry, the original purpose of its importation into the United States. The species tolerance of noxious emissions of gases and various dusts assures its continued use for plantings in industrial environments. Tolerance of poor soils and low soil moisture dictates its selection for city plantings in arid climates as well as shelterbelt plantings and on strip mine reclamation projects, although its unfavorable traits (odor and root sprouting) have decreased city plantings. Root sprouting into fields is also a problem in shelterbelt plantings.

Pollinating insects are attracted by the male flowers. Honey from ailanthus has been reported as having an initial foul taste that disappears with aging, resulting in an exceptionally good tasting honey *(13)*.

Genetics

In the two centuries since its introduction into North America, ailanthus has probably become differentiated into genetically different subpopulations based on seed traits. Seed characteristics of ailanthus have been identified as traits that differentiate varieties and geographical strains. Ailanthus with bright red samaras compared to the more common greenish yellow has been named *Ailanthus altissima* var. *erythrocarpa* (Carr.) Rehd. A study of 11 seed sources from California and Eastern States found that seed width and weight were correlated with latitude *(6)*. Northern sources have wider, heavier seed than the more southern sources.

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Alnus glutinosa (L.) Gaertn. European Alder

Betulaceae Birch family

David T. Funk

European alder *(Alnus glutinosa)*, also called black alder or European black alder, was introduced to eastern North America in colonial times. This tree ranges in size from a large shrub to a large tree. It has escaped cultivation and grows naturally on low-lying lands. Its rapid growth, tolerance for acid soils, and nitrogen-fixing role make European alder desirable for shelterbelts, reclamation areas, landscapes, and biomass production. It is valuable to wildlife for providing good cover and a source of seeds.

Habitat

Native Range

European alder has a broad natural range that includes most of Europe and extends into North Africa, Asia Minor, and western Siberia *(82)*. Densest distribution is in the lowlands of northern Germany, northern Poland, White Russia, and the northwestern Ukraine *(33)*. The species is locally naturalized throughout the northeastern United States and maritime Canada.

Climate

The duration of low winter temperature limits the range of European alder in Scandinavia because the species does not extend into regions where the mean daily temperature is above freezing for less than 6 months of the year. The southeastern boundary of European alder distribution in Eurasia corresponds closely with the 500 mm (20 in) annual rainfall line *(60)*. European alder is hardy to winter temperatures of -54° C (-65° F) *(36)*, but apparent winter damage to young European alder plantings in North Carolina resulted in partial to complete dieback of 80 percent of the trees. Relatively early low temperatures in November and December were probably responsible for the damage, rather than extreme cold, as the overwinter minimum was only -18° C (0° F) *(9)*.

Soils and Topography

European alder grows well on acid soils, and its growth is reduced under the alkaline or near-neutral conditions that are desirable for many other species. During their first growing season in most types of soils alder seedlings form root nodules that are the site of nitrogen fixation. Seedlings already nodulated grow satisfactorily when outplanted on sites with pH as low as 3.3; plants not already nodulated usually die under these very acid conditions *(27,77)*. Nodules develop satisfactorily at pH as low as 4.2 *(8)*, but seedlings were stunted and had poor root systems and chlorotic leaves when grown in clay soil with pH between 8.0 and 8.5 *(63)*. Optimum soil pH for nodulation appears to be between 5.5 and 7.0 *(35)*. Spoil-bank plantations in Ohio and Kentucky verify the minimum pH for satisfactory European alder growth as about 3.4 *(30,55)*. On very acid (pH 2.9) coal spoils in Indiana, alder survival, growth, and root nodule weight were all increased by liming sufficient to raise pH to at least 6.1 (eventually declining to 4.8) *(41)*. In a greenhouse experiment using acidic Pennsylvania mine spoil, alders did not respond to lime amendments until phosphorus was also added *(89)*.

Both nodulated and nonnodulated alders require molybdenum for nitrogen metabolism *(6,42)*; adequate amounts of Mo are present in most soils, although it may not be available on strongly acid sites. On sites with poor internal drainage, European alder can tolerate iron concentrations normally toxic to many plants *(44)*. On tidal flats adjacent to the English Channel, the chlorine concentration of the soil solution in the root zone of mature alders occasionally rises to 5 percent of that of sea water immediately following equinoctial high tides *(78)*.

European alder is responsive to differences in soil moisture *(5,40)*, and growth often is notably better on lower slopes than on upper slopes. Alder utilizes intermittently moist sites very well *(56)*. It is "a species of stream and lake sides and ... soils of impeded drainage throughout the British Isles," although not topographically limited to such sites if rainfall is high *(60)*. Even though alder tolerates heavy soils better than most trees, reduced soil oxygen (especially below 5 percent) inhibits root nodulation and the growth of nodulated plants *(57)*.

In a species with such a broad natural range, altitudinal distribution is bound to be related to latitude. European alder is found at sea level at the northern limits of its range, up to 300 m (985 ft) in Norway, 600 m (1,970 ft) in the Harz Mountains of Saxony, 850 m (2,790 ft) in the Bavarian Mountains, 1300 m (4,270 ft) in the Tyrol and in Greece, and 1800 m (5,900 ft) in the Caucasus *(60,88)*. The most

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common soils on which it grows in North America occur in the orders Histosols, Inceptisols, and Entisols.

Associated Forest Cover

Natural alder communities include ash, birch, willow, and oak, "forming ash-alder wood on low-lying ground of high soil fertility and moisture, alder-willow thickets in areas liable to seasonal flooding, and alder-birch wood on higher lying, less fertile, generally acid soils.... Pure stands are...common, but not as extensive in Britain as, for example, in northwest Germany" *(60)*. European alder and gray willow, *Salix cinerea atrocinerea*, form a tidal woodland near the upper limits of a salt marsh on the Cornish coast. In the absence of disturbance, the alder-willow community succeeds the marsh *(78)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—European alder is monoecious; flowers of both sexes emerge from buds that begin to develop about 9 to 10 months before pollination. These preformed buds allow an early estimate of the following year's seed crop. Male buds are distinctly longer than female buds—about 1 cm (0.4 in) compared to about 3 mm (0.1 in)—and grow nearer the tips of branchlets. They remain green until December and grow intermittently throughout the winter *(74)*. Female flowers are 1 to 1.5 cm (0.4 to 0.6 in) long when mature; male catkins are from 5 to 13 cm (2 to 5 in) long. They vary in color from tree to tree, over a range from light peach to deep purple. Occasional bisexual catkins are found.

A general calendar of seed formation is as follows *(61,74)*: Styles begin to form in July, year 1; rest period follows from August, year 1 to February, year 2; pollination occurs in February to March, year 2; placenta forms in May, year 2; ovules form in June, year 2; ovary begins to grow from June to July, year 2; embryo sacs are formed in July, year 2; fertilization takes place from late July to early August, year 2; embryo grows throughout August, year 2; embryo ripens throughout September and germination first becomes possible during this month. Seeds are mature when their pericarps turn brown, although the cones remain green until the seeds are released.

As an exception to this calendar, pollination is sometimes delayed until early April in the northeastern United States. The flowering schedule is typically dichogamous.

Most European alder trees are virtually self-sterile *(61)*, but certain selfed trees have produced seed with germination percentages as high as 8 percent *(81)*. Viability of cross-pollinated seed ranged from 8 to 90 percent *(61,81)*. Viability of pollen was greater than 99 percent at the time of collection *(61)* but fell to about 1 percent after 50 days storage *(73)*. Individual trees in Iowa set a good crop of seed every year, but the percentage of filled, viable seed ranged from 0 to 90 percent. Because fertilization occurs in July and August, the developing embryo may be especially vulnerable to heat and moisture stress. Seed with little or no viability was produced in years of severe summer drought *(37)*.

Seed Production and Dissemination—In Europe, alder may not produce a uniform seed crop every year *(61)* but abundant crops are frequent *(56)*. Plantations in the eastern United States seem to bear out both points: seed crops do vary from year to year and they are generally rather heavy. European alder (fig. 1) is precocious; some trees begin to flower at the beginning of their second growing season and by their sixth or seventh year are producing large

Figure 1—*Collecting seeds from a European alder tree in southern Illinois. At age 14 this tree was 16 m (51 ft) tall and 24 cm (9.3 in) in d.b.h.*

quantities of seeds. Several hundred strobiles may develop on a 6- to 9-m (20- to 30-ft) tree, and in summer and early autumn the mass of maturing fruit approximates the mass of foliage *(74)*. Seeds average 60 per catkin *(60)*. The seeds are very small brown nuts, ranging from about 240,000/kg (110,000/lb) *(56)* to as many as 1,400,000/kg (635,000/lb) *(87)*.

Seeds begin to fall in late September or early October and the best seeds usually fall first *(11,92)*. Seed dispersal continues throughout the winter. Very few alder seeds remain viable beyond the first germination season *(62)*. Seed production as high as 18 kg/ha (16 lb/acre) has been achieved in a 14-year-old grafted orchard in southwestern Germany; yields of 5 to 13 kg/ha (4.5 to 12 lb/acre) were more typical *(54)*.

Although European alder seeds can germinate immediately after they are shed, stratification and cold treatment enhance their germination capacity *(85)*. Seeds collected before strobiles turn brown require several months of afterripening to germinate *(60)*. Epigeal germination in the nursery is prompt; it begins 10 to 20 days after spring sowing and is essentially complete within 2 weeks. Germination is notably better at pH 4 than at higher or lower pH *(85)*.

Production of containerized alder seedlings allows them to be inoculated with *Frankia* and assures their nodulation prior to planting. A 1 to 1 ratio of peat and vermiculite in the potting mix is recommended *(7)*.

European alder seeds have no wings; therefore, despite their small size they are usually not spread more than 30 to 60 m (100 to 200 ft) by the wind, although they may occasionally be blown much farther over the top of crusted snow. Where wind is the only likely means of dissemination, alder saplings are rarely found more than 20 to 30 m (65 to 100 ft) from the parent tree. The seeds contain an air bladder and float in water, and McVean holds that rather than wind, running water and wind drift over standing water are the principal agents of dispersal *(62)*. Naturalized European alder stands in the United States are most commonly found adjacent to streams.

Seedling Development—Seeds buried more than 0.5 cm (0.2 in) deep germinate satisfactorily but many of the new seedlings fail to emerge *(62)*. The soil need not be saturated to gain good seed germination, but high air humidity is essential. In regions with only 50 to 65 cm (20 to 25 in) of annual rainfall, alder seedlings will only establish where the surface soil falls within the capillary fringe of the water table so that it remains constantly moist for 20 to 30 days in the spring (March to May)" *(63)*.

Alder seedlings can survive, although not thrive, under conditions of flooding that would kill off the seedlings of most other forest trees. In a British experiment, seedlings did not live indefinitely with their entire root systems completely submerged and were quickly killed by such treatment during the growing season. Nevertheless, when the water level was maintained flush with the top of the soil, the more robust seedlings were able to produce adventitious roots at the soil surface and their growth was hindered very little *(63)*. The original roots of European alder can grow actively during periods of flooding lasting for as long as 1 week and resume growth after longer periods of flooding *(31)*. In another greenhouse study, alder seedlings were successfully grown in oxygen-free soil, outperforming white willow (*Salix alba*) under such conditions *(10)*.

Growth of young potted European alder seedlings was not inhibited by addition of foliage litter of six herbaceous species that did inhibit growth of black locust (*Robinia pseudoacacia*). Alder seedling growth and root nodulation were more than doubled by addition of crownvetch (*Coronilla varia*) litter *(49)*.

A light intensity equivalent to about 5 percent of full daylight is essential for first-year alder establishment; for survival in subsequent years about 20 percent of full daylight is required *(63)*. "First-year seedlings and 2- to 3-year-old plants up to 5 cm (2 in) in height are frequent in some woods, but complete internal regeneration is seldom seen. Regeneration tends to be peripheral, or to occur with the formation of an even-aged stand" *(60)*.

Natural alder seedlings in Croatia grow to be about 0.5 m (1.7 ft) tall in their first year *(32)*, but seedlings in American nurseries are not always as large.

Alder seedlings are associated with actinomycetes and mycorrhizae. Development of nitrogen-fixing root nodules in European alder is induced through root-hair infection by actinomycetes of the genus *Frankia*. Actinomycetous endophytes isolated from European alder are cross-infective with other *Alnus* species and even other genera such as sweetfern (*Comptonia*) and bayberry (*Myrica*) *(38)*. Thus, even though European alder is not native to the United States, suitably infective actinomycetes may be available wherever it is planted *(20)*. On the other hand, in a greenhouse study, European alders inoculated with native European endophytes grew six times faster than those inoculated with a *Comptonia* isolate *(59)*. Strongly infective *Frankia* strains are not necessarily effective in stimulating rapid alder growth, and those that produce spores may be weakly parasitic, rather than symbiotic *(58)*.

European alder has been found associated with at least six mycorrhizal fungi. Suitable symbionts appear to be widely available, as both ectomycorrhizae and endomycorrhizae were found on root samples taken from European alder plantations in Iowa, on coal strip mines in Ohio, and on kaolin spoils in Georgia *(38)*. Ecto-, endo- and ectendomycorrhizae were described as associated with European alder on Bohemian lignite spoil banks. The endomycorrhizae were found only below 10 cm (4 in) depth *(66)*.

Vegetative Reproduction—European alder commonly sprouts from the stump after cutting, and live branches can be layered successfully. Root suckers are rare *(60)*. In coastal southern Sweden, alders live to maximum age of 100 years but frequently produce basal sprouts and form multi-stemmed stumps following death of the original stem *(18)*.

Air-layering of alder shoots has been 89 to 100 percent successful *(84)*. The rooting ability of greenwood cuttings of European alder seedlings less than 4 years old was found to be generally high; over an 18- to 20-month period, 100 to 200 cuttings were successfully rooted from each ortet *(25)*.

Alnus glutinosa can be readily propagated by *in vitro* tissue culture. Plantlets of several clones were rooted within 3 weeks, subsequently transferred to soil mix, and maintained in good physiological state for as long as 4 years *(90)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Height growth begins in mid-April and continues through July or August. Saplings may continue growing into September or October *(59,101)*. In the mountains of Czechoslovakia, 90 percent of diameter growth takes place between mid-May and mid-August, a growing season almost identical to that of European beech (*Fagus sylvatica*) *(12)*. In Switzerland, alder root growth commenced about 4 days after the beginning of vegetative bud swelling and about 5 weeks before the beginning of branch extension growth *(51)*. Root growth resumes in October and continues throughout the winter except when the ground is frozen *(79)*.

Height growth of alder seedlings planted on rather acid (pH 4.3 to 4.5) strip-mined land in Ohio falls between normal yield values (table 1) for site classes I and II at age 16 *(29)*. On a moderately permeable bottom-land site in southern Illinois, 9-year-old European alder outgrew predicted height values and averaged 11.2 m (36.8 ft) tall, and 13.7 cm (5.4 in) in d.b.h. *(72)*. Height growth slowed markedly *(80)* over

Table 1—Height and basal area growth of European alder in Germany *(88)*

	Site class					
	I		II		III	
Age	Height	Basal area	Height	Basal area	Height	Basal area
yr	*m*	*m²/ha*	*m*	*m²/ha*	*m*	*m²/ha*
20	15	17	11	14	9	[illegible]
30	18	22	15	18	12	[illegible]
40	21	25	17	20	14	[illegible]
50	23	27	19	22	15	[illegible]
60	24	28	20	23	16	[illegible]
70	25	29	21	24	17	18
80	26	30	21	24	—	—
yr	*ft*	*ft²/acre*	*ft*	*ft²/acre*	*ft*	*ft²/acre*
20	49	74	36	61	29	48
30	59	96	49	78	39	61
40	69	109	56	87	46	70
50	75	118	62	96	49	74
60	79	122	66	100	53	78
70	82	126	69	105	56	78
80	85	131	69	105	—	—

Table 2—Height growth of European alder in Croatia *(32)*

	Seedlings			Sprouts		
Age	Annual growth	Total height	Mean annual growth	Annual growth	Total height	Mean annual growth
yr				*m*		
2	0.6	1.1	0.5	1.1	2.0	1.0
4	0.8	2.6	0.6	1.5	4.8	1.2
6	1.1	4.7	0.8	1.1	7.1	1.2
8	1.3	7.3	0.9	1.0	9.1	1.1
10	1.4	10.1	1.0	0.9	11.0	1.1
12	1.3	12.7	1.1	0.9	12.7	1.1
14	1.0	14.8	1.1	0.8	14.3	1.0
16	0.8	16.5	1.0	0.7	15.8	1.0
18	0.5	17.6	1.0	0.7	17.2	0.9
20	0.4	18.5	0.9	0.6	18.4	0.9
yr				*ft*		
2	1.9	3.6	1.8	3.5	6.6	3.3
4	2.7	8.5	2.1	4.9	15.8	3.9
6	3.6	15.3	2.5	3.5	23.4	3.9
8	4.4	23.8	3.0	3.2	29.9	3.7
10	4.6	33.0	3.3	3.0	36.0	3.6
12	4.2	41.6	3.5	2.8	41.7	3.5
14	3.3	48.6	3.5	2.6	47.0	3.4
16	2.5	54.0	3.4	2.4	51.9	3.3
18	1.8	57.9	3.2	2.2	56.3	3.1
20	1.3	60.7	3.0	1.9	60.3	3.0

the next 5 years in this widely spaced plantation, and at age 14 the trees averaged 12.3 m (40.4 ft) tall and 20.1 cm (7.9 in) in d.b.h. (table 2). European alder usually reaches two-thirds of its maximum height by age 25 *(33)* but may survive for 120 years on the best sites, growing to be at least 1 m (3 ft) in diameter *(60)*. The root wood of European alder has lower specific gravity than the stem wood but longer fibers with thinner walls *(100)*. In an Ohio stripmine plantation, stem wood specific gravity averaged 0.39 and did not vary with age or geographic origin of the trees. Fiber length increased from 0.71 mm (0.28 in) at age 5 to 0.93 mm (0.36 in) at age 17 *(83)*.

Representative percent chemical composition of European alder from two points of view has been reported. The first was based on total aboveground biomass, 4-year-old trees *(104)*; the second was based on leaf litter from four stands *(69)*:

	N	P	K	Ca	Mg	Mn
Biomass	0.80	0.60	0.30	0.63	0.07	0.02
Litter	2.68	0.05	0.15	0.20	0.23	—

Rooting Habit—Alder has been characterized as possessing an extensive root system of both surface and deep branches, which enables it to survive on either waterlogged soils or those with a deep water table *(60)*. In Germany, European alder is considered to be the deepest rooting indigenous tree species *(86)*. Alder's deeply penetrating taproots often extend well below normal water table; if the water level falls, these roots are well situated to use deep-lying soil moisture not available to the upper portion of the root system. This may explain alder's outstanding success on spoil banks *(37,64)*.

Generally, there are two kinds of alder root nodules. One is a large, perennial, usually single nodule sometimes 5 cm (2 in) or more in diameter *(21)* and most often situated near the root crown. These nodules may persist as long as 10 years, with those in the 4- to 5-year age class making up the greatest proportion of the weight of nodules per tree *(1)*. The other type is ephemeral, much smaller—typically 1.5 to 3 mm (0.06 to 0.12 in) in diameter—and generally distributed throughout the surface root system. Becking found that molybdenum-deficient alder plants formed many small nodules of much reduced total dry weight and exhibited associated nitrogen deficiency. Plants with an adequate molybdenum supply had mainly single large nodules *(6)*.

The most striking effect of alders on soil is nitrogen enrichment. Not only is alder leaf litter rich in nitrogen *(68)*, but many nitrogenous compounds are heavily concentrated in alder roots and root nodules *(99)*. In European alder seedlings, rate of nitrogen fixation is closely related to nodule fresh weight and total plant dry weight, suggesting that selection for growth should also achieve gains in nitrogen fixation *(4)*. In Quebec, 3- and 4-year-old alders planted at 33 cm by 33 cm (13 in by 13 in) spacing fixed nitrogen at an annual rate of 53 kg/ha (47 lb/acre) *(15)*.

Fixation of atmospheric nitrogen by alders takes place in root vesicles *(67)* and nodules *(8)*. In a greenhouse experiment, maximum nitrogen fixation in young European alder plants occurred in late August; throughout the growing season about 90 percent of the nitrogen fixed was steadily transferred from the nodules to the rest of the plant *(91)*. In an alder grove growing on peat in the Netherlands, nitrogen fixation was also found to peak in August *(1)*.

European alder (as well as other *Alnus* species) differs from most deciduous tree species in retaining much foliar nitrogen in the leaves until they fall *(17)*. In a southern Illinois plantation, nitrogen content of leaves decreased by only one-sixth from midsummer until leaf fall. At the time of the last collection, in mid-November, leaf nitrogen content was about 2.6 percent; thus there was a substantial quantity of nitrogen to be dropped in the leaf litter *(21)*.

In Finland, a 13-year-old European alder plantation and a 55-year-old natural stand were sampled for 4 years. Alder litter averaged 2690 and 3705 kg/ha (2,400 and 3,305 lb/acre) per year (ovendried), respectively, and contributed about 82 percent of the total annual litter production. Total nitrogen content of the leaf litter averaged 77 kg/ha (69 lb/acre) per year, reaching a high of 101 kg/ha (90 lb/acre) in 1 year in the plantation. NH_4-nitrogen in the upper 3-cm layer of soil rose from 180 mg/kg (180 p/m) before leaf fall to 270 mg/kg (270 p/m) after leaf fall, indicating that at least part of the nitrogen of alder leaf litter was rapidly mineralized *(69)*.

Prodigious amounts of litter can accumulate under alder stands. For instance, 10 species of pines and deciduous trees were planted on a Kentucky strip mine with and without alternate rows of European alder. After 10 years, 28.7 t/ha (12.8 tons/acre) of litter accumulated in the plantings without alder, while 61.7 t/ha (27.5 tons/acre) built up under the stands with a 50 percent alder component. The relative contribution of alder leaf fall and increased litter production of the other species, stimulated by the alder, could not be determined. In the spring of the 10th growing season, the pH of the spoil beneath the stand containing alder was significantly lower than the plantings without alder. Similarly, the concentration of total soluble salts was consistently higher, both spring and fall, in the stands with alder than in those without *(75)*.

European alder leaf litter readily gives up water-soluble organic substances, losing 12 percent of its dry weight after only 1 day's leaching in cold water. Alder litter was also found to decompose faster than that of beech or oak *(70)*. The C:N ratio of alder foliage suspended in a stream declined rapidly from 19 to about 13 within a month after leaf fall, then more slowly to 11 (near the effective mineralization optimum) after 6 months *(13)*.

Other components of alders also accumulate considerable nitrogen. In a plantation on a good alluvial site in western Kentucky the following nitrogen contents (percent dry weight) were measured at the end of the fourth growing season (adapted from *104*):

Foliage	3.15
Branches	1.02
Bolebark	1.10
Bolewood	0.26
Total tree (aboveground)	0.79

Even young alders can fix and add significant amounts of nitrogen to soil. A Padus silt loam in Wisconsin averaged 966 mg/kg (966 p/m) of nitrogen in the upper 4 cm (1.5 in) of dry soil before 1-year-old European alder seedlings were planted. After two growing seasons, soil nitrogen (at the same depth) had increased 222 mg/kg (222 p/m) in soil immediately adjacent to the alders and by 158 mg/kg (158 p/m) at a distance of 15 cm (6 in) *(39)*.

Reaction to Competition—"The alder is primarily a pioneer and opportunist species, and is capable of direct colonization of even the rawest of soil material.... The species acts as a pioneer on hydroseres, being capable of colonizing at very early stages in the primary succession if good seed is available. Alder carr (deciduous woodland or scrub on a permanently wet, organic soil) does not succeed an earlier *Salix* and *Rhamnus* carr, though these species may colonize simultaneously, and pure alder carr eventually results from the greater vigour and longevity of the alders" *(65)*.

In central Switzerland, alder is considered to be more shade tolerant than willow *(Salix* spp.), larch *(Larix* spp.), poplar *(Populus* spp.), birch *(Betula* spp.), or Scotch pine *(Pinus sylvestris)*; equal in tolerance to ash *(Fraxinus* spp.); and less tolerant than eastern white pine *(Pinus strobus)* or Douglas-fir *(Pseudotsuga menziesii)* *(50)*. Overall, it is classed as intolerant of shade *(18)*.

In Yugoslavia and Germany, European alder is grown on 40- to 80-year rotations, depending on intensity of thinning and products desired. The stand is clearcut at the end of the rotation and replanted with 1-year seedlings or 1-1 transplants.

Nursery practice for European alder is fairly routine, and 1-year seedlings are usually large enough for outplanting. Liberal irrigation following sowing is essential for good seed germination.

Alder has generally beneficial effects on associated plants. Part of the nitrogen fixed by alders soon becomes available to other species in mixed stands, especially through mineralization of nitrogen leached from litter. Norway spruce *(Picea abies)* grown in pots with European alder "obtained nitrogen fixed in the root nodules of alder although leaves falling in autumn were always carefully removed" *(98)*.

In a 3-year-old Wisconsin plantation, hybrid poplars in a plantation spaced at 1.2 by 1.2 m (3.9 by 3.9 ft) grew 21 percent taller in a 1:2 mixture with European alder than when grown without alder (4.9 m versus 4.0 m; 16.0 ft versus 13.1 ft). This growth increase corresponded closely with that achieved through optimal ammonium nitrate fertilizer treatment, which stimulated a 24 percent increase *(39)*. Similar results were obtained in Quebec where mixed plantings of two alders per poplar yielded slightly more total biomass at age 3 than pure alder plantings and 50 percent more than pure hybrid poplar *(16)*.

European alder often is recommended for use in mixed plantings with other species on nitrogen-poor sites. On strip-mined sites in eastern Kentucky, 10 coniferous and broadleaved species were grown in alternate rows with European alder at 2.1 by 2.1 m (6.9 by 6.9 ft) spacing; after 10 years, trees grown in mixture with alder were 11 to 84 percent taller and 20 to 200 percent larger in diameter than the same species grown without alder *(75)*.

In northern Bohemia, *Populus* × *berolinensis* used for strip-mine reclamation averaged 12.5 m (41 ft) tall at age 14 in pure plantings but grew to 14 m (46 ft) in mixture with *Alnus glutinosa*; poplars in the mixed planting were also much straighter *(24)*.

In southern Indiana, European alder seedlings were interplanted into a 2-year-old plantation of black walnut *(Juglans nigra)* on well-drained silt loam soil. Ten years after interplanting, walnuts grown in mixture with alder averaged 5.3 m (17.5 ft) tall against 4.2 m (13.8 ft) in pure stands; alder stimulated an increase in walnut diameter from 5.6 cm (2.2 in) to 6.9 cm (2.7 in) *(14)*. In contrast, at four locations in Illinois and Missouri, alder interplanted with walnut suddenly declined and died after 8-12 years. Allelopathy caused by juglone was the only cause of death that could be substantiated *(80)*.

Damaging Agents—In a Scottish plantation survey, European alder suffered less damage by deer browsing and rubbing than did birch, willow, or other hardwood species *(2)*. In contrast, deer browsed more than half the European alder seedlings in a 2-year-old plantation in Pennsylvania; damage was much less on Japanese larch (*Larix leptolepis*), white spruce (*Picea glauca*), eastern white pine, and red pine (*Pinus resinosa*) *(26)*.

Dozens of insects and diseases have been observed on European alder but few cause serious damage. Among pests recognized as potentially troublesome is the striped alder sawfly, *Hemichroa crocea*, a native of Europe that is now found across northern United States and Canada. It produces two generations per year. From July through September larvae occasionally eat all of the alder leaves except the midrib and larger veins *(93)*.

The European alder leafminer, *Fenusa dohrnii*, is another introduced species. It makes blotch mines on alder leaves in the northern United States and southeastern Canada *(5)*. The alder flea beetle, *Altica ambiens alni*, feeds on both surfaces of alder leaves from Maine to New Mexico. It is sometimes a pest of alders in recreational areas and along roadsides *(93)*. The woolly alder aphid, *Prociphilus tesselatus*, is distributed throughout the eastern United States and is often abundant on alder. Although it causes little direct damage, it is suspected of weakening the trees and providing infection courts for subsequent fungal attack.

Several fungus species have been isolated from *Alnus glutinosa* trees that died back following woolly aphid infestations. They include *Botryodiplodia theobromae* *(76)* which has not been confirmed as pathogenic. In an *A. glutinosa* seed production plantation in Kentucky, *Phomopsis alnea* caused basal stem cankers and eventual mortality as great as 17 percent *(71)*. In northern Mississippi, occasional alder trees infested with woolly aphids are heavily damaged by sapsuckers *(103)*. Alder seems to be very resistant to chronic ozone fumigation *(45)*; in contrast, it is more susceptible to SO_2 damage than most species *(94)*.

Special Uses

European alder is valuable for wildlife. Because the cones open gradually and release seed throughout the winter, they are a dependable source of food for seed-eating birds such as pine siskins and goldfinches. European alder is recommended for use in shelterbelts to provide cover for pheasants. When combined with *Prunus laurocerasus* and *Sorbus aria*, it makes a compact planting suitable for establishment adjacent to cropland *(34)*.

Alders have been recommended for afforestation of disturbed areas throughout much of the temperate world *(46,52)*. Their tolerance of low pH and their rapid growth, abundant leaf litter production, and ability to fix atmospheric nitrogen combine to make European alder especially desirable for planting on spoil banks, which typically contain little organic matter and available nitrogen.

Establishing European alder on mined sites apparently improves their suitability for earthworm habitat. Ten adult *Lumbricus terrestris* worms were released in a 4-year-old *A. glutinosa* plantation growing on calcareous coal spoil in southern Ohio. After 5 years the population had increased to 60/m² (6/ft²) as far as 15 m (50 ft) from the point of introduction and was apparently still increasing, with obvious desirable implications for hastening soil development *(97)*.

Alder is useful in urban forestry. A system for producing containerized alder seedlings suitable for park and roadside planting has been described. Trees grown in Iowa according to these methods averaged 94 cm (37 in) tall after only 8 months *(19)*.

Biomass use of European alder has potential. On a river terrace site in northern Alabama, 6-year-old European alder produced more than six times as much volume per tree as sycamore (*Platanus occidentalis*) of the same age *(22)*. Alders in southern Illinois, planted at only 998 trees per hectare (404/acre) on a bottom-land site, produced 54.7 t/ha (24.4 ton/acre) at age 9 (dry weight of entire tree, above ground) *(72)*. Alder may be a more promising species to grow in short-rotation, intensive-culture plantations for cattle feed. Protein yield was nearly that of alfalfa *(3)*.

Aboveground parts of European alder have energy values of about 5 Kcal/g (9,000 Btu/lb) dry weight. Calorific value of branchwood is 10 percent greater than that of bolewood *(43)*.

Genetics

Population Differences

In an extensive progeny test of select European alder parent trees, heritability of height growth was good at age 7. Most good clones performed consistently when used as either male or female parents. The general superiority of alders from the moraine region of upper Bavaria was confirmed *(102)*.

Races and Hybrids

Over the broad range of European alder, racial development is to be expected, but within regions, variation is sometimes slight. Fifteen European alder provenance collections, grown on calcareous spoil banks in southern Ohio for 16 years, differed sharply in both growth and survival. Most of the trees originated in central and north–central Europe; survival was best for three seedlots of central German provenance. Trees from Diessen, Bavaria, grew to be 21 percent taller and 20 percent larger in diameter than the plantation mean and averaged 0.57 m (1.87 ft) per year in height growth over the past 10 years. Alders of Uppland, Sweden, provenance were almost complete failures, being only 3.5 m (11.5 ft) tall with 11 percent survival after 16 years *(29)*.

The 16-year results reported above are reasonably consistent with those at age 6, with one striking exception. Trees from Peiting, Bavaria, formerly second tallest in the plantation *(28)*, have virtually collapsed, with survival declining to 37 percent, and height growth over the past 10 years least of all except for the trees from Uppland, Sweden *(29)*. Similar results are reported from European alder trials in the Netherlands, where trees from three German seed sources grew rapidly for 7 years and then slowly for the following 3 years *(96)*. The need for caution in making early selections is obvious.

In a larger but younger provenance trial in Pennsylvania, most trees burst buds with a 4-day period well before the beginning of the frost-free season. Most of the fastest growing trees originated from the central part of the species' natural distribution. About half the variation in total height was due to rate of growth; the other half was due to length of the growing season *(23)*.

European alders that grow fastest are more likely to be single-stemmed. At age 6 in the Ohio test, the correlation between height and number of stems per tree was -0.31 *(28)*.

European alder hybridizes readily with many other alders. Particularly vigorous hybrids have been reported for *A. cordata* × *A. glutinosa (48)*, *A. glutinosa* × *A. incana (47)*, *A. glutinosa* × *A. rubra (53)*, and *A. glutinosa* × *A. orientalis (95)*.

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Alnus rubra Bong. Red Alder

Betulaceae Birch family

Constance A. Harrington

Red alder (*Alnus rubra*), also called Oregon alder, western alder, and Pacific coast alder, is the most common hardwood in the Pacific Northwest. It is a relatively short-lived, intolerant pioneer with rapid juvenile growth. The species is favored by disturbance and often increases after logging and burning. Because the commercial value of alder has traditionally been lower than that of its associated conifers, most forest managers have tried to eliminate the species from conifer stands. On the other hand, red alder is the only commercial tree species west of the Rocky Mountains with the capability to fix atmospheric nitrogen, and the species is now being considered for deliberate use in some management systems (*19*).

Habitat

Native Range

Red alder is most often observed as a lowland species along the northern Pacific coast. Its range extends from southern California (lat. 34° N.) to southeastern Alaska (60° N.) (fig. 1). Red alder is generally found within 200 km (125 mi) of the ocean and at elevations below 750 m (2,400 ft). It seldom grows east of the Cascade Range in Oregon and Washington or the Sierra Nevada in California, although several isolated populations exist in northern Idaho (*36*).

Climate

Red alder grows in climates varying from humid to superhumid. Annual precipitation ranges from 400 to 5600 mm (16 to 220 in); most of the precipitation is rain in winter. Summers are generally cool and dry. Temperature extremes range from -30° C (-22° F) in Alaska and Idaho to 46° C (115° F) in California. Low winter temperatures and lack of precipitation during the growing season appear to be the main limits to the range of red alder. For good development of trees, either annual precipitation should exceed 630 mm (25 in) or tree roots should have access to ground water.

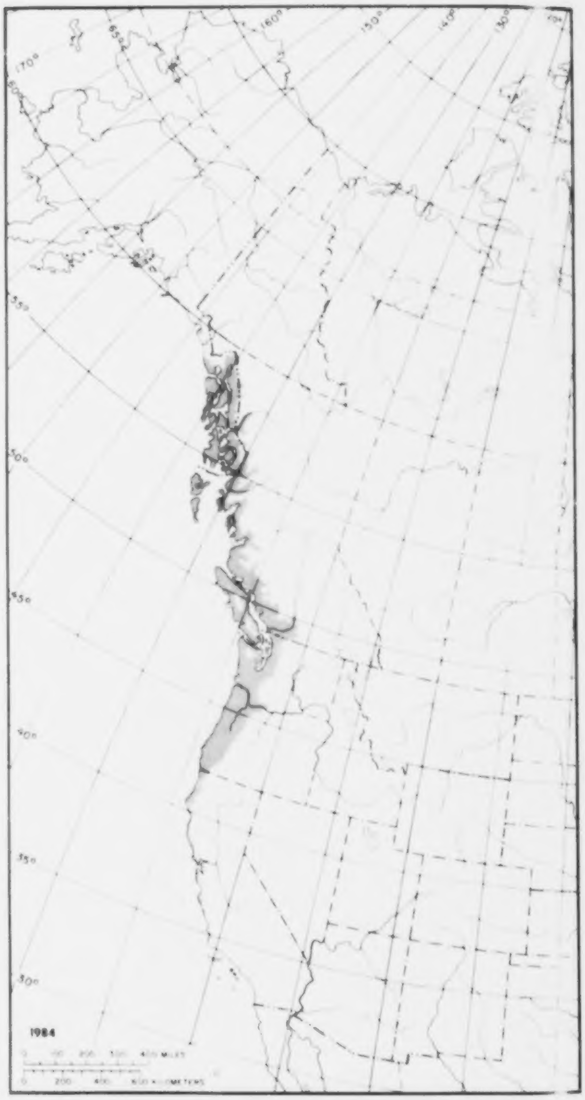

Figure 1—*The native range of red alder*

Soils and Topography

Red alder is found on a wide range of soils, from well-drained gravels or sands to poorly drained clays or organic soils. It grows primarily on soils of the orders Inceptisols and Entisols but is also found on

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some Alfisols, Ultisols, and Histosols. Best stands are found on deep, well-drained loams or sandy loams of alluvial origin; however, some excellent stands are also found on residual or colluvial soils derived from volcanic materials.

Soil moisture during the growing season appears to influence where the species grows. Alder can tolerate poor drainage conditions and some flooding during the growing season; consequently, it prevails on soils where drainage is restricted—along stream bottoms or in swamps or marshes. It is not commonly found on droughty soils, however; and in areas of low precipitation, it seldom grows on steep south or southwest-facing slopes. In Idaho and California, stands are usually limited to borders of streams or lakes.

Red alder develops best on elevations below 450 m (1,480 ft) in northern Oregon, Washington, and British Columbia. In Alaska, red alder generally occurs close to sea level. Farther south, scattered trees are found as high as 1100 m (3,610 ft), but most stands are at elevations below 750 m (2,460 ft).

Associated Forest Cover

Red alder grows in both pure and mixed stands. Pure stands are typically confined to stream bottoms and lower slopes. Red alder is, however, much more widely distributed as a component of mixed stands. It is a major component of the forest cover type Red Alder (Society of American Foresters Type 221) and occurs as a minor component in most of the other North Pacific cover types *(11)*.

Common tree associates are Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, western redcedar *(Thuja plicata)*, grand fir *(Abies grandis)*, Sitka spruce *(Picea sitchensis)*, black cottonwood *(Populus trichocarpa)*, bigleaf maple *(Acer macrophyllum)*, and willow *(Salix* spp.). Occasional tree associates include cascara buckthorn *(Rhamnus purshiana)*, Pacific dogwood *(Cornus nuttallii)*, and Oregon ash *(Fraxinus latifolia)*. Western paper birch *(Betula papyrifera* var. *commutata)* is an occasional associate in the northern portion of the range of alder, and redwood *(Sequoia sempervirens)* in the southern portion.

Common shrub associates include vine maple *(Acer circinatum)*, red and blue elder *(Sambucus callicarpa, S. cerulea)*, Indian plum *(Osmaronia cerasiformis)*, salmonberry *(Rubus spectabilis)*, western thimbleberry *(R. parviflorus)*, devilsclub *(Oplopanax horridum)*, Oregongrape *(Berberis nervosa)*, and salal *(Gaultheria shallon)*.

Herbaceous associates include stinging nettle *(Urtica dioica)*, skunkcabbage *(Lysichitum americanum)*, blackberries *(Rubus laciniatus, R. leucodermis)*, California dewberry *(R. ursinus)*, swordfern *(Polystichum munitum)*, lady fern *(Athyrium filix-femina)*, Pacific water parsley *(Oenanthe sarmentosa)*, youth-on-age *(Tolmiea menziesii)*, Oregon oxalis *(Oxalis oregana)*, and western springbeauty *(Montia sibirica)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red alder reaches sexual maturity at age 3 to 4 years for individual trees and age 6 to 8 for most dominant trees in a stand *(5)*. It is generally monoecious, with separate male and female catkins developing on the previous year's twigs *(22)*. Staminate catkins occur in pendulous clumps. In late winter they elongate, changing from green to reddish brown and from 2 to 3 cm (1 in) long to about 7 or 8 cm (3 in). Pistillate catkins also occur in clumps but are borne upright. They are 5 to 8 mm (0.2 to 0.3 in) long and reddish green when receptive. Flowering occurs in late winter or early spring; peak shedding of pollen generally precedes peak receptivity by only a few days. Most alder seed is probably the result of outcrossing, but some self-pollination does occur *(5)*.

Seed Production and Dissemination—Red alder is a prolific and consistent producer of seed. Moderate seed crops are produced almost annually and bumper crops occur every 3 to 5 years. Complete failure of a seed crop is rare, but after a severe freeze in November 1955, almost no seed was produced in 1956 *(43)*.

The seeds are small, winged nuts borne in pairs on the bracts of woody, conelike strobili *(33)*. The strobili are 11 to 32 mm (0.4 to 1.3 in) long, and 8 to 15 mm (0.3 to 0.6 in) wide. Seed dispersal begins in late September in the middle of the species' range, somewhat earlier in Alaska, and several weeks later in California. Most of the seeds are shed during late fall and winter. For minimum loss of seeds, cone collection should begin in September in Alaska and continue until December in California.

Red alder seeds are very light, numbering 800 to 3,000/g (22,900 to 85,700/oz), and wind dissemination is effective. The seed can be carried long distances by wind, and abundant seed for natural regeneration is usually present throughout the range of red alder.

Seedling Development—Red alder germinates and grows well on moist mineral soil with full sunlight [illegible]. Germination is epigeal. Seedlings can become established from seeds that fall on a highly organic surface, such as forest litter. Because the seeds are so small, however, their food reserves are minimal and the tender radicle must encounter a moist, nutritious substrate almost immediately after germination if the seed is to become an established plant. Seedlings can tolerate partial shade for several years, but after that full sun is required for normal development.

Red alder can be regenerated by any method that provides full sunlight and exposed mineral soil. The species is an aggressive pioneer on avalanche paths, road cuts, log landings, skid trails, or other areas where mineral soil has been freshly exposed to seed fall. Clearcutting and large-group selection are feasible regeneration systems. During harvesting or in a subsequent site preparation treatment, the site must be disturbed sufficiently to expose mineral soil. Fire can probably substitute for mechanical disturbance on most sites. To exclude red alder from the next rotation stand, some forest managers try to reduce the supply of alder seed by cutting possible alder seed trees in the vicinity before or at the time of final harvest, and also to avoid creating favorable seedbed conditions by disturbing the site as little as possible during logging and, if feasible, by not burning the logging slash.

Artificial regeneration can be accomplished with either bare-root or containerized seedlings. Dried, stored seed need not be stratified *(2,29)*. Nursery production of seedlings is fairly trouble free if standard techniques are used; sowing should generally be done fairly late (in June), however, to prevent the development of seedlings too large to be easily handled by planting crews. If the soil is sterilized, it may be necessary to reinoculate it to speed formation of mycorrhizae and root nodules. Guidelines for producing containerized seedlings are available *(2)*, covering seed treatment, inoculation methods, and growth media. Survival and growth of planted seedlings are usually excellent.

Height growth of red alder seedlings is exceptionally rapid. On favorable sites, seedlings can grow 1 m (3.3 ft) or more the first year and on all but the poorest sites, seedlings surpass breast height (1.37 m; 4.5 ft) the second year *(16)*. Maximum annual height growth of more than 3 m (9.8 ft) a year can be achieved by 2- to 5-year-old seedlings *(16)*.

Seasonal growth of red alder is under strong climatic control and consequently quite variable. The timing of radial growth is similar for red alder and its common associate Douglas-fir; in the Puget Sound area of Washington State, growth begins about mid-April and continues until mid-September *(32)*. Height growth begins slightly later in the season than radial growth. Red alder has indeterminate height growth; thus, height growth continues through the growing season until soil moisture, temperature, or light conditions become unfavorable.

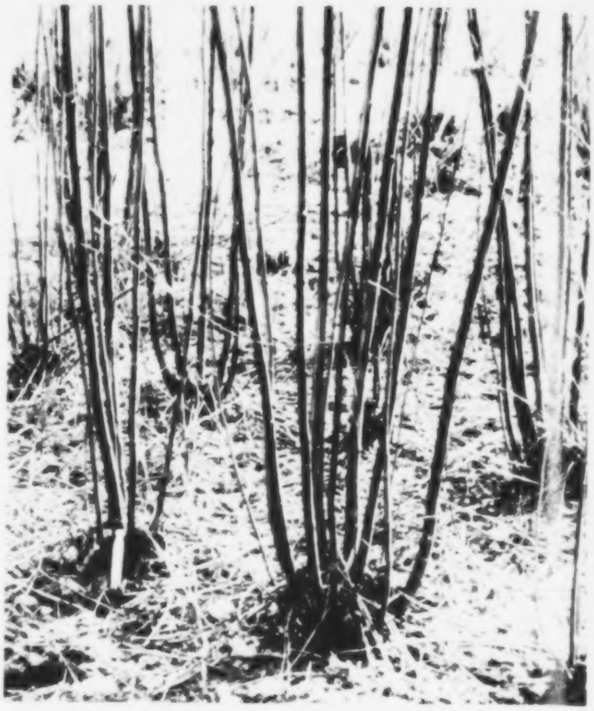

Figure 2—*Sprouts on 6-year-old red alder rootstocks previously cut at ages 2 and 4. Stake is 18 cm (7 in).*

Vegetative Reproduction—Red alder sprouts vigorously from the stump when young. It can be repeatedly coppiced on short cycles but rootstock mortality increases with each harvest *(17)* (fig. 2). Age, time of year, and cutting height influence the likelihood of obtaining stump sprouts and the vigor of the sprouts *(15)*. Stumps will sprout best when trees are cut in the winter and when stump height exceeds 4 in (10 cm). Older trees rarely sprout and coppice regeneration cannot be expected after pole-size or saw-log-size material is harvested *(15)*.

Greenwood cuttings from young trees can be readily rooted. More than 50 percent of cuttings from 1- to 3-year-old plants took root within 6 weeks after treatment with 4,000 to 8,000 p/m indole-3-butyric acid and 10 percent benomyl *(27)*. The cuttings were set in a well-aerated planting mix and placed in a warm environment (22° to 25° C; 72° to 77° F) in the daytime and 16° to 22° C (61° to 72° F) at night with high relative humidity and a 16-hour photoperiod.

Cuttings of succulent new spring growth from shoots of 3- to 6-year-old trees and epicormic sprouts from 27- to 34-year-old trees have also been rooted successfully *(30)*. Best results were obtained with a

10-second dip in 2,000 or 4,000 p/m indole-3-butyric acid. The extent of rooting and root vigor on the cuttings varied greatly among ortets and treatments.

Red alder can also be propagated by mound layering *(11)*. For this technique the seedlings are first coppiced. When the sprouts are a few months old, the stump and the base of the sprouts are covered with soil. The sprouts soon form roots; they can be severed from the stump and planted at the end of the first growing season.

Sapling and Pole Stages to Maturity

Growth and Yield—Red alder has rapid juvenile growth; of its associates, only black cottonwood grows as much or more during the juvenile phase. On good sites, trees may be 9 m (30 ft) at age 5, 16 m (52 ft) at age 10, and 24 m (79 ft) at age 20. One tree was 9.8 m (32.1 ft) tall and 16.3 cm (6.4 in) in d.b.h. 5 years from seed *(36)*. Mean annual production in 7- to 12-year-old thickets has been estimated (oven-dry) at 15.4 t/ha (6.8 tons/acre) *(5)*.

Growth slows after the juvenile stage, the decrease beginning much sooner on poor sites. Site index as determined at base age 20 years ranges from 10 to 25 m (33 to 82 ft) *(16)*; at base age 50, it ranges from 18 to 37 m (60 to 120 ft) *(44)*. Associated conifers have much slower juvenile growth, but they sustain height growth years longer than alder. On an average site, both Douglas-fir and red alder can attain the same height at about age 45 *(36)*. Beyond that age, Douglas-fir surpasses red alder in height.

Red alder is a relatively short-lived species, maturing at about 60 to 70 years; maximum age is usually about 100 years *(45)*. On favorable sites, trees can be 30 to 40 m (100 to 130 ft) tall and 55 to 75 cm (22 to 30 in) in diameter. A record-size tree measured 198 cm (78 in) in d.b.h., but trees over 90 cm (35 in) in diameter are rare. Maximum cubic volume is attained at age 50 to 70 (500 m^3/ha or 7,150 ft^3/acre) *(5,44)*. In pure stands on good sites, it has been estimated that red alder can achieve annual cubic volume growth rates of 21 m^3/ha (300 ft^3/acre) in pulpwood rotations of 10 to 12 years, and 14 m^3/ha (200 ft^3/acre) in saw-log rotations of 30 to 32 years *(5)*. Most of the existing alder volume is in mixed stands where growth and yield are variable.

Rooting Habit—Red alder forms extensive, fibrous root systems. Root growth of seedlings is rapid; 2-year-old nursery-grown seedlings have to be planted using a shovel because of their wide-spreading, large, woody roots.

Red alder roots are commonly ectomycorrhizal. Only a few species of fungi, however, are capable of forming ectomycorrhizal associations with alder. Fungal symbionts include an alder-specific fungus (*Alpova diplophloeus*) and fungi capable of mycorrhizal associations with other hosts (*Paxillus involutus*, *Astraeus pteridis*, and *Scleroderma hypogaeum*) *(26)*.

Red alder also has root nodules that fix atmospheric nitrogen. The nodules are a symbiotic association between the tree and an actinomycete (*Frankia* spp.). Nodulation occurs soon after seed germination; root systems of seedlings a few months old commonly have dozens of visible nodules, ranging from the size of a pinhead up to 25 mm (1 in) in diameter. Mature trees have nodules on both the large woody roots and the smaller new roots. Nodules found on large trees can be as large as 80 or 90 mm (3.1 or 3.5 in) in diameter.

Reaction to Competition—Red alder requires more light than any of its tree associates except black cottonwood and is classed as intolerant of shade. Young seedlings can withstand partial shade for a few years but will grow very little; if not released, the seedlings will die. The only trees that survive are those that maintain dominant or codominant crown positions. Self-thinning or mortality caused by competition is rapid, and mean densities in natural stands decrease from 124,000 seedlings per hectare (50,000/acre) at age 5 *(7)* to 1,665 seedlings per hectare (675/acre) at age 20 *(44)*. Red alder also self-prunes extremely well. Shaded lower branches rapidly die and fall off; alder boles are typically clear and slightly tapered (fig. 3). Live crown ratios in crowded, pure stands are very low, and narrow, domelike crowns are characteristic.

Early control of spacing is necessary to keep live crown ratios high enough to maintain good growth beyond the juvenile phase. Saw-log yields can be maximized on short rotations by combining early spacing control with pulpwood thinnings *(5)*. Thinnings in previously unthinned stands are most effective in stimulating growth of residual trees if done before height growth slows—about age 15 to 20 *(5,28,39)*. Thinning in older stands can salvage mortality and help maintain the vigor of residual trees but does not usually accelerate diameter growth *(25,40)*.

Epicormic branching has been reported after thinning, especially when thinning has been late or drastic *(1,40)*. Epicormic sprouting is most commonly observed on the south side of stressed trees. Epicormic branches appearing after early thinning are usually ephemeral and not cause for concern.

Red alder can be grown in either pure or mixed stands. Creation or maintenance of mixed stands requires careful attention to the respective height-growth patterns and tolerances of the species. Alder must be kept in the upper canopy to survive in mixed stands.

Damaging Agents--Red alder is fairly free from most insect and disease problems, especially when young (age 40 or 50) and uninjured *(21,45)*. *Phellinus igniarius*, a white heart rot, is probably the major cause of cull in older trees. Three canker-causing stem diseases—*Didymosphaeria oregonensis*, *Hymenochaete agglutinans*, and *Nectria galligena*—cause some damage, especially in young stands, but their overall impact is slight. Red alder has a number of foliage and catkin diseases, but none are economically important. Many species of fungi have been identified on alder; but, except for those discussed above, they tend to be secondary invaders on dead or dying tissue. Wood stain and decay proceed rapidly in cut trees, and logs should be processed soon after harvest unless they are stored in fresh water *(43)*. During intermediate cuts, care must be taken to avoid injuring residual trees; once trees are injured, decay organisms can invade rapidly.

Insect pests are not usually a major concern, but serious outbreaks of some defoliators can cause growth reductions. The forest tent caterpillar *(Malacosoma disstria)*, western tent caterpillar *(M. californicum)*, alder woolly sawfly *(Eriocampa ovata)*, striped alder sawfly *(Hemichroa crocea)*, the alder flea beetle *(Altica ambiens)*, and a leaf beetle *(Pyrrhalta punctipennis)* have caused substantial damage; but reports of mortality are rare *(5,13,45)*. A flatheaded wood borer *(Agrilus burkei)* can kill twigs and branches *(5,13)*. The alder bark beetle *(Alniphagus aspericollis)* breeds primarily in slash and in young stressed trees; however, healthy trees can be attacked when bark beetle populations are high *(5)*. Ambrosia beetles *(Gnathotrichus retusus, Trypodendron lineatum, Xyleborus saxeseni)* attack logs and slash left on the ground, causing rapid degrade in quality. Insect holes can also serve as entry sites for fungi. Merchantable material should be removed rapidly, and large accumulations of slash should be avoided.

Animals cause only minor damage in alder stands. Young trees are occasionally browsed by black-tailed deer, especially during the late summer and fall *(6)*, but alder is not a preferred species. Mountain beaver sometimes girdle small stems and branches; their use of alder foliage for food is minor and sporadic except in late September when use is fairly heavy *(38)*. In years of high populations, meadow mice girdle young stems. Damage by meadow mice has been most commonly observed in grassy or very wet areas.

Climatic factors can damage red alder. Mortality and top damage have been documented in natural stands after ice storms or unseasonable frosts *(10,45)*. Fire is rarely a damaging agent because of the scarcity of flammable debris in alder stands. In fact, the species sometimes has been planted as a firebreak to protect adjacent conifers *(45)*. Alder bark is thin but sufficiently fire resistant to prevent damage during light surface fires *(43)*. Windthrow is not common in alder because of the intermingling of roots and branches, the absence of leaves during winter storms when soils can be waterlogged, and the relatively deep-rooting habit of the species on well-drained soils. Uprooted trees are most commonly observed along cutting boundaries or where established root systems have been undercut by flooding or erosion.

Special Uses

Red alder wood is diffuse-porous, moderately dense, and uniformly textured. It is used in the production of solid wood products, such as furniture, cabinets, case goods, pallets, and novelties *(31)*; composite products, including plywood and flakeboard *(5)*; and fiber-based products, such as tissues and writing paper.

Alder is a common fuelwood and is burned both in home fireplaces and stoves, and in mills that use

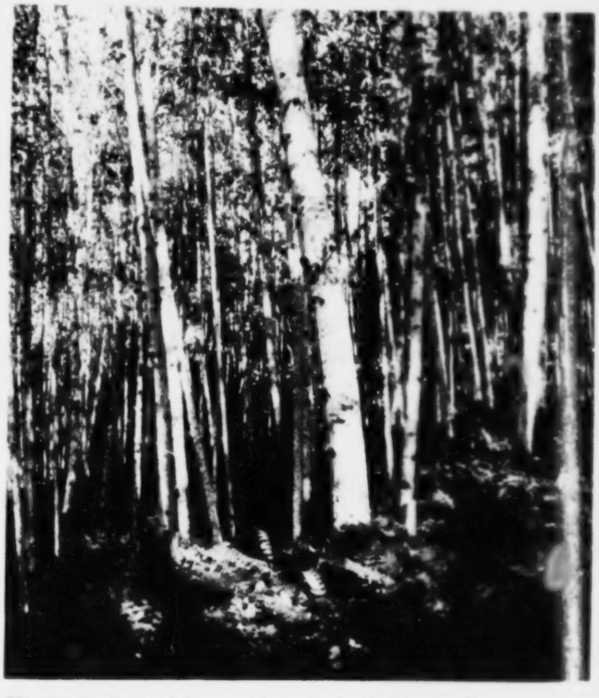

Figure 3—*Dense, 28-year-old, natural red alder stand.*

residues to produce heat for drying and other processes *(31)*. Because of its rapid juvenile growth and ability to coppice, red alder has been evaluated for use in biomass farms for energy conversion *(5)*; some experimental plantings have been made to evaluate yields under intensive management.

The ability of red alder to fix atmospheric nitrogen can result in increases in both nitrogen content and its availability in the soil. Nitrogen fixed in the nodules is added to the soil in four ways: direct excretion from living roots or nodules, decomposition of dead roots or nodules, leaching from foliage, and decomposition of litter rich in nitrogen. Fixation rates vary diurnally and seasonally *(37)* and with site and stand age *(3,36)*. Maximum annual fixation rates of 320 kg/ha (290 lb/acre) (*36*, based on accretion) in pure stands and 130 kg/ha (120 lb/acre) (*3*, based on acetylene reduction assays) in mixed stands have been reported.

Red alder also increases the organic matter content in the soil *(34,36)*. Concomitant with increases in soil organic matter, decreases in soil bulk density and pH have been reported *(4,34,36)*.

Red alder has been proposed for use alone and in both crop rotation and mixture with other species *(8)*. Because of its ability to add nitrogen and organic matter to a site and its rapid juvenile growth on a variety of sites, the species has been experimentally planted as follows: (a) to serve as a nitrogen source for other species (particularly Douglas-fir and black cottonwood) *(5,9)*; (b) on coal mine spoils, landslides, and other eroded or low fertility areas *(20,35)*; (c) for streambank or roadside protection; (d) in areas of poor drainage; (e) as a firebreak or windbreak *(5,34)*; and (f) for wildlife areas.

An additional experimental use of red alder in a crop rotation system is to plant it in areas containing coniferous root pathogens, such as *Phellinus weiri*, which can survive for many years in organic materials in the soil *(14)*. The only known control is to replace the disease-susceptible species with a nonsusceptible species for 40 to 50 years. Red alder is a good candidate for such an interim species.

Other experimental uses of alder include addition of foliage, twigs, and sawdust to grain or alfalfa for cattle feed and addition of sawdust to nursery soils to increase organic matter.

Genetics

Population Differences

Population differences in height growth, diameter growth, stem form, bark thickness, and resistance to frost or insect attack have been demonstrated in a provenance trial in coastal Oregon involving 10 sources from the range of red alder *(5)*. High growth rates were positively correlated with good form but negatively correlated with resistance to spring frosts. Differences among provenances in bole volume or aboveground biomass were greater than differences in height or diameter alone *(24)*. Specific gravity did not differ significantly among provenances, nor was it correlated with growth rate *(17)*.

The fastest growing trees in the provenance trial were from northwestern Washington, but trees from British Columbia, southwestern Washington, and Oregon also grew well. The slowest growing trees were from Alaska and Idaho. Thus, it appears reproductive material of red alder can be moved to mild sites over fairly long distances along the Pacific coast.

Differences in form and in characteristics of branch, bark, and wood among eight stands in western Washington have also been assessed *(5)*. Variability among trees in a stand was high; only bark thickness, a branch diameter index, branch angle, and a crown-width index differed significantly among stands.

A cut-leaf variety (*Alnus rubra* var. *pinnatisecta*) is found in a few isolated areas in British Columbia, Washington, and Oregon. The cut-leaf characteristic is caused by a single recessive gene *(42)*; thus, the cut-leaf variety can be used as a marker in genetic breeding studies *(5)*.

Families varied in their height-growth response to water-table depth in a 24-family progeny trial in western Washington *(23)*. Use of genotypes tolerant of waterlogging may enhance growth of red alder on wet sites.

Phenotypic variation between trees is high. Studies are underway to assess genotypic variation and the heritability of various traits. An individual tree approach for selection has been recommended for tree improvement programs. Because red alder has extensive populations of even-aged stands and because of its reproductive and growth characteristics, the species has the potential for rapid genetic gains *(5)*.

Races

No races of red alder have been described. Races may exist, however, especially in the disjunct populations or in the extremes of the range. One researcher has divided the species into three populations (northern, central, and southern) on the basis of vegetative and reproductive features from herbarium specimens *(12)*.

Hybrids

No natural hybrids have been documented, but possible hybrids with *Alnus tenuifolia* and *A. rhom-*

bifolia have been described where the ranges of these species overlap in Idaho *(36)*. Red alder has been successfully crossed with *A. cordata*, *A. glutinosa*, *A. japonica*, and *A. sinuata (5)*.

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Arbutus menziesii Pursh　Pacific Madrone

Ericaceae　Heath family

Philip M. McDonald and John C. Tappeiner, II

Pacific madrone (*Arbutus menziesii*) is one of the most widely distributed tree species native to the Pacific coast. Named for its discoverer, Archibald Menzies, a 19th century Scottish physician and naturalist, the species is called arbutus in Canada, and madrone, madroña, or madroño in the United States. The latter name is ascribed to Father Juan Crespi, chronicler of the 1769 Portola expedition.

Although examples of fine furniture and attractive veneer from madrone are common, utilization is far below potential and management is almost nil.

Habitat

Native Range

Pacific madrone (fig. 1) ranges from the east coast of Vancouver Island and the immediate mainland of British Columbia (lat. 50° N.) southward to near Palomar Mountain, San Diego County, CA (lat. 33° N.), a north–south distance of about 1880 km (1,170 mi). The species is common along the western slopes of the Coast Ranges in Washington, Oregon, and California, southward to San Luis Obispo County, CA. It is abundant throughout much of the Klamath Mountains of Oregon and California, and from Yuba County, CA, southward through Calaveras County in the Sierra Nevada.

Climate

In western British Columbia, Washington, and Oregon, the climate best suited to Pacific madrone is characterized by mild temperatures with prolonged cloudy periods, narrow diurnal fluctuation, and limited extremes. Average January temperatures range from 2° to 8° C (36° to 46° F) and average July temperatures from 10° to 20° C (50° to 68° F). Winters generally are wet and mild, and summers cool and relatively dry with long frost-free seasons. Average annual precipitation is usually abundant, ranging from 790 to more than 3000 mm (31 to 118 in), 75 to 85 percent of which is received between October 1 and March 1, mostly as rain.

In the interior valleys and hills of the Klamath Mountains and lower west slopes of the southern Cascades, average January temperatures range from 2° to 5° C (36° to 41° F) and average July temperatures from 17° to 25° C (62° to 77° F). Average annual precipitation varies between 760 and 890 mm (30 and 35 in). The average January temperature in the heart of the Pacific madrone range in the Sierra Nevada is 5° C (41° F), and the average July temperature is 22° C (72° F). Average annual precipitation is 1730 mm (68 in).

In the Coast Ranges of California, temperatures where Pacific madrone grows average 2° to 5° C (36° to 41° F) in January and 15° to 20° C (59° to 68° F) in July. Average precipitation varies between 1140 and 1650 mm (45 and 65 in) yearly in the north to 640 to 760 mm (25 to 30 in) in the south. Some fog usually is present throughout this region.

Within the total range of this species, temperature extremes are from -21° to 46° C (-6° to 115° F) and annual rainfall from 460 to 4220 mm (18 to 166 in) *(30)*.

Soils and Topography

Soils on which Pacific madrone is found are derived from glacial deposits of porous sands and gravels and hard till in the north, through volcanic tuffs and metamorphosed sedimentary and volcanic rocks in the Klamath Mountains, to volcanic and sedimentary rocks in the California Coast Ranges. Granitic and metavolcanic rocks support the species in the Sierra Nevada. Most Pacific madrones are found on Alfisols, followed to a much lesser extent by Ultisols and Inceptisols. The soils show a wide range of textures, varying from fine-textured loams and clay loams to coarse-textured sandy loams and gravelly clay loams. Rocky soils are common, and many are less than 1 m (3.3 ft) deep. A common soil characteristic is good internal drainage and low moisture retention in summer.

Many extensive soil series have been identified as supporting Pacific madrone (table 1). In California, madrone has been found on more than 30 soil series.

Pacific madrone grows on a variety of terrain from nearly level flats and gently sloping benches to steep mountainsides. Often it is found in canyons near creeks and rivers. In general, madrone grows on all aspects but is found most often on those facing south and west. In southern California, however, madrone

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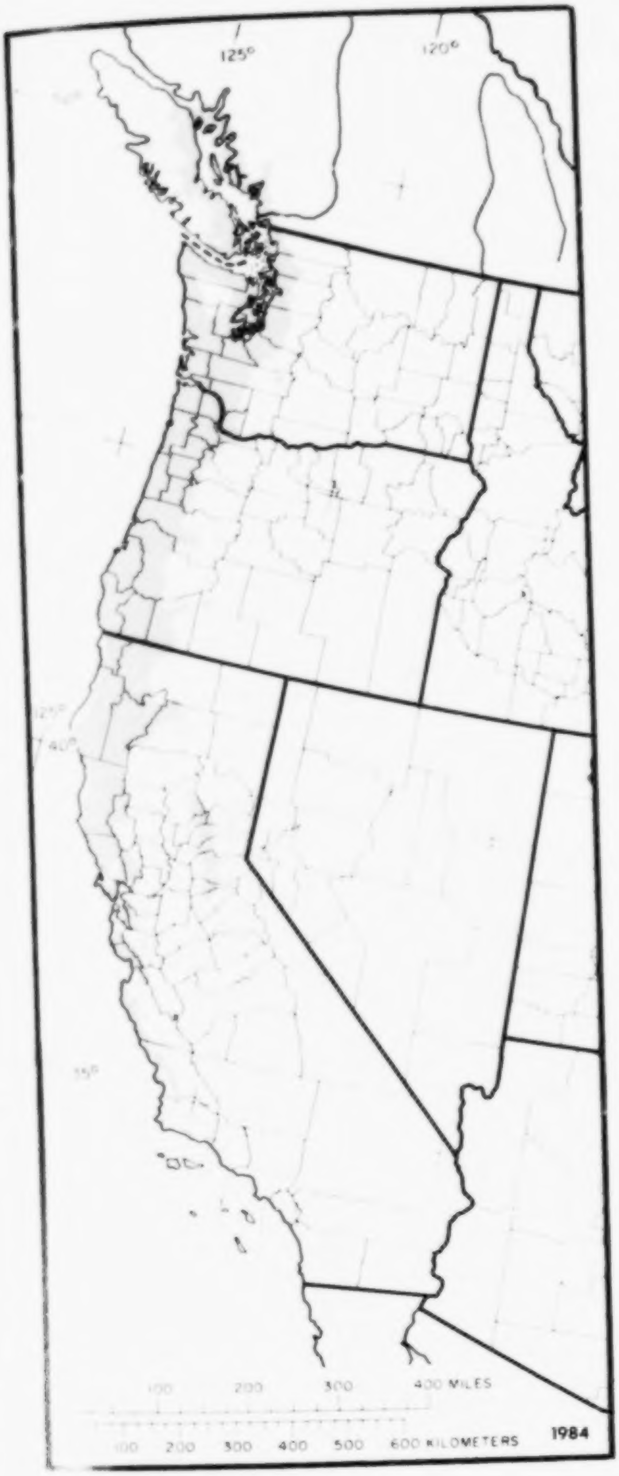


Figure 1—*The native range of Pacific madrone.*

Table 1—Principal mountain ranges and soil series where Pacific madrone is found

Mountain range	Soil series
British Columbia Washington and Oregon Coast	Astoria, Everett, Hoodsport Melbourne, Olympic, Spanaway
Klamath and southern Cascade	Boomer, Hugo, Josephine Neuns, Pollard, Ruch Sheetiron, Siskiyou
California	
North Coast	Hely, Hoda, Hugo Larabee, Madonna, Orick
Central Coast	Felton, Junipero, Sheridan, Sur
Sierra Nevada	Aiken, Cohasset, Holland Mariposa, Marpa, McCarthy Musick, Sites
Transverse and	Crouch, Shaver

often is abundant in cool canyons—about the only place in this area where the species is found.

In the northern part of its range, Pacific madrone grows at or near sea level, extends up rivers, and inhabits mountain slopes to the 915 m (3,000 ft) elevation. The species ranges from 455 to 915 m (1,500 to 3,000 ft) and, occasionally, to 1435 m (4,700 ft) in the Klamath Mountains. In the California Coast Ranges, Pacific madrone grows well from 245 to 1300 m (800 to 4,260 ft). It is found from about 365 to 1065 m (1,200 to 3,490 ft) in the Sierra Nevada but is more common between 700 and 975 m (2,300 and 3,200 ft). At the southern end of its range in the Transverse and Peninsular Mountains, madrone grows from 610 to 1065 m (2,000 to 3,490 ft).

Associated Forest Cover

Pacific madrone is a major component of the forest cover type Douglas-fir–Tanoak–Pacific Madrone (Society of American Foresters Type 234) *(4)*, and an associated species in a wide variety of others including Pacific Douglas-Fir (Type 229), Douglas-Fir–Western Hemlock (Type 230), Port Orford-Cedar (Type 231), Redwood (Type 232), Pacific Ponderosa Pine (Type 245), Pacific Ponderosa Pine–Douglas-Fir (Type 244), Sierra Nevada Mixed Conifer (Type 243), Knobcone Pine (Type 248), California Live Oak (Type 255), Canyon Live Oak (Type 249), Oregon White Oak (Type 233), and California Black Oak (Type 246).

The Douglas-Fir–Tanoak–Pacific Madrone forest cover type is characterized by Douglas-fir as the overstory species and tanoak and madrone as secondary canopy. Regardless of stand structure and species mix in earlier stages of succession, the relative position of Pacific madrone at maturity is constant. The proportion of tanoak and madrone in the secondary canopy, however, varies widely. Higher proportions of madrone usually are found in drier locales, particularly on south aspects *(14)*.

Fossilized leaves of a species similar to modern-day Pacific madrone have been found in northwestern Nevada, the Blue Mountains of Oregon, and Tuolumne County, CA. This species and associated flora date to the Miocene epoch of 12 to 26 million years ago. In terms of species composition, the flora resembles the oak-madrone forest of the central coastal mountains in California today *(2)*.

In western British Columbia, Washington, and Oregon, Pacific madrone intermingles extensively with Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, Oregon white oak *(Quercus garryana)*, red alder *(Alnus rubra)*, and bigleaf maple *(Acer macrophyllum)*. Common associates in the Klamath Mountains and southern Cascades are Douglas-fir, ponderosa pine *(Pinus ponderosa* var. *ponderosa)*, California black oak *(Quercus kelloggii)*, and Oregon white oak, with sugar pine *(P. lambertiana)*, tanoak *(Lithocarpus densiflorus)*, California white fir *(Abies concolor* var. *lowiana)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, canyon live oak *(Q. chrysolepis)*, knobcone pine *(P. attenuata)*, and bigleaf maple locally present.

In the northern and central California Coast Ranges, Douglas-fir, tanoak, redwood *(Sequoia sempervirens)*, coast live oak *(Quercus agrifolia)*, canyon live oak, and California-laurel *(Umbellularia californica)* mix with Pacific madrone. Common associates in the southern California mountains are Coulter pine *(Pinus coulteri)*, interior live oak *(Quercus wislizenii)*, California black oak, canyon live oak, coast live oak, and bigcone Douglas-fir *(Pseudotsuga macrocarpa)*.

Smaller trees *(11)* that are common throughout the range of Pacific madrone from Vancouver Island or immediate mainland of British Columbia southward through Washington, Oregon, and northern California are vine maple *(Acer circinatum)*, Rocky Mountain maple *(A. glabrum)*, black hawthorn *(Crataegus douglasii)*, Pacific bayberry *(Myrica californica)*, Sitka alder *(Alnus sinuata)*, bitter cherry *(Prunus emarginata)*, western serviceberry *(Amelanchier alnifolia)*, Pacific rhododendron *(Rhododendron macrophyllum)*, Pacific dogwood *(Cornus nuttallii)*, western dogwood *(C. occidentalis)*, red-osier dogwood *(C. stolonifera)*, Pacific willow *(Salix lasiandra)*, Scouler willow *(S. scoulerana)*, Pacific red elder *(Sambucus callicarpa)*, blue elder *(S. cerulea)*, and California hazel *(Corylus cornuta* var. *californica)*. Others, too numerous to mention, have more limited distributions within madrone's natural range.

Pacific madrone grows individually or in groves. It rarely forms large stands, and pure stands of any size are seldom seen. Madrone often is associated with two or more hardwood species in groups interspersed among conifers. The groups can be large or small, however, depending on the size of logged units or burns. In California's central Coast Ranges, mixed hardwood stands are extensive over a large portion of the forested landscape *(24)*.

Occasionally, Pacific madrone forms a woodland with other conifer and hardwood associates. In the valleys of the Umpqua and Rogue Rivers of southwestern Oregon, California black oak, Oregon white oak, and Pacific madrone form a stunted open cover on the low rounded hills. Scattered Douglas-firs occasionally are present *(6,26)*.

Several investigators have placed Pacific madrone and associated species along measured decreasing moisture gradients in the field. In coastal northern California, madrone ranked fourth of 10 species in ability to extract moisture from the soil. Another investigator placed madrone first of 10 species for this ability in the central western Cascade Range of Oregon. Plainly, madrone is found in drier environments.

Madrone also was ranked by other environmental variables. Relative to 20 northwestern tree associates, madrone was listed in the group of four species judged best adapted to warm temperatures. Further, madrone was in a group that placed fifth to seventh of 23 species ranked from high to low in tolerance of drought *(15)*. At least one author described the species as being resistant to ice damage because water quickly ran off the waxy leaves and did not freeze on them. Another stated that heavy wet snowfalls place brittle-limbed madrone at a disadvantage. The species was judged the least frost-resistant tree native to British Columbia. Occasionally, madrones in Washington and Oregon are damaged by severe frosts.

Shrub associates are fairly numerous, as could be expected for a species with a large natural range; they are greenleaf manzanita *(Arctostaphylos patula)*, whiteleaf manzanita *(A. viscida)*, bearberry *(A. uva-ursi)*, Oregongrape *(Berberis nervosa)*, buckbrush *(Ceanothus cuneatus)*, deerbrush *(C. integerrimus)*, squawcarpet *(C. prostratus)*, snowbrush *(C. velutinus)*, salal *(Gaultheria shallon)*, oceanspray *(Holodiscus discolor)*, pachistima *(Pachistima myrsinites)*, huckleberry oak *(Quercus vaccinifolia)*, western poison-oak *(Toxicodendron diversilobum)*, Sierra gooseberry *(Ribes roezlii)*, wood rose *(Ros* *gymnocarpa),* thimbleberry *(Rubus parviflorus),* salmonberry *(R. spectabilis),* trailing blackberry *(R. ursinus),* spreading snowberry *(Symphoricarpos acutus),* creeping snowberry *(S. mollis),* and evergreen huckleberry *(Vaccinium ovatum).* Only occasionally, as in the California north Coast Range forests, is the shrub layer dense *(24).* Both the shrub and herb communities tend to be sparse under mature stands.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowers of Pacific madrone are small, whitish, perfect, and urn-shaped. They are borne in dense racemes of terminal panicles. Madrone flowers in mid-March at lower elevations with warm temperatures, and in mid-May at higher elevations. Flowering usually ends in June.

The fruit, a berry 8 to 12 mm (0.3 to 0.5 in) in diameter, has a dry mealy flesh and generally is five-celled. Fruits mature from mid-September to mid-November. Ripe berries are bright red or reddish-orange. Yellowish-orange or even yellowish-green berries, however, also may be present in the same cluster at the same time. Number of seeds per berry ranges from 2 to 37, averaging about 20.

Seed Production and Dissemination—Pacific madrone is described as providing abundant fruit almost every year *(23).* On a good site in the Sierra Nevada from 1958 through 1977, however, bumper seed crops were produced in 2 years, light crops in 8 years, and little or no seed in 10 years. Berry production during a light seed year for three representative trees, 23, 36, and 41 cm (9, 14, and 16 in) in breast-height diameter, ranged from 13,320 to more than 107,000 per tree and seemed to relate best to the amount of living crown *(12).*

Pacific madrone first produces berries at 3 to 5 years *(23).* In the northern Sierra Nevada, the dominant sprout in a 4-year-old clump produced 62 berries. Trees 60 to 160 years old produce heavy seed crops if healthy, but the age at which berries no longer are produced is unknown.

Freshly picked red and yellow berries from the northern Sierra Nevada were weighed and numbers of berries and seeds counted. Berries numbered 1,390 to 2,490/kg (630 to 1,130/lb), and seeds 434,310 to 705,470/kg (197,000 to 320,000/lb) *(23).*

Pacific madrone berries are disseminated by gravity and consumers. Because the berries are heavy, they fall directly beneath tree crowns, generally into a thick layer of tough leathery leaves. They do not bounce or roll far. Animals, however, often carry the berries farther away from tree crowns. Madrone berries are prized as food by birds, rodents, deer, and wood rats. At least five species of birds, especially the mourning dove and band-tailed pigeon, devour berries. More than 17 percent of this pigeon's November diet and 11 percent of its December diet were madrone berries. Stomach analysis of one pigeon indicated that it had eaten 111 berries—so many that it could not fly *(25).* In the northern Sierra Nevada, snap traps baited with a single red berry caught more white-footed deer mice than those with peanut butter and wheatflakes *(12).*

Seedling Development—Germination of Pacific madrone seed is epigeal and has been described as both moderately high and fair. A test in California gave 55 percent germination after 3 months stratification at 2° to 5° C (36° to 41° F). Two other investigators recommended 3 months of stratification. A laboratory study on seed from the Sierra Nevada, however, indicated that a shorter stratification period might be adequate: seed stratified at 2° C (36° F) for 30 to 40 days with no other treatment produced 94 percent germination. Immersing seed in concentrated sulfuric acid for 1 minute before stratification also gave good results, but applying heat for 1 hour at 95° C (203° F) and then stratifying seriously impaired germination *(12).*

To evaluate seedling establishment under more natural conditions, germinating seeds in a laboratory were buried in unsterilized sandy loam and no fungicide was applied. Damping-off fungi killed most of the seedlings, and after 11 months, only 6 percent survived. Trials of seedlings from madrone berries in the laboratory and field also indicated high losses from damping-off fungi.

A comprehensive study in the Santa Cruz Mountains of central coastal California *(20)* showed that fungus attack directly killed 28 percent of madrone seedlings. An additional 22.7 percent mortality, however, was attributed to mild drought preceded by crippling from root decay fungi. Most of the remaining seedling mortality was caused by invertebrates, chiefly slugs. These pests were particularly lethal to seedlings in deep shade. None of the 276 seedlings on shady plots survived.

Losses of seedlings on sunny plots in the semi-open forest were caused mainly by fungi. Only 2 percent of the seedlings on these plots survived to August 2 of the year in which they germinated. In southwestern Oregon, all Pacific madrone seeds germinated the first year after seeds ripened. However, seedlings began to die immediately after emergence and most had died after 1 year. Cause of death, in descending order, was lack of soil moisture, litterfall, damping off, and invertebrates. First-year mortality was 90 to 100 percent *(29)*.

In general, Pacific madrone seedlings are not abundant. They usually become established in disturbed areas, along road cuts, on bare mineral soil at the base of uprooted trees, or in semi-open forests. In the northern Sierra Nevada, seedlings are established mainly along partially shaded road cuts or in small shaded openings. Occasionally, they become established beneath woody shrubs or small trees in clearcuttings. In southwestern Oregon, percent survival after 3 years, although low, was higher in clearcuttings than in young and old stands *(29)*. The most favorable seedbed for establishment seems to be bare mineral soil free from all, or nearly all, organic material. The notable lack of madrone seedlings beneath madrone trees could be the result of toxic metabolites being formed as an end product of the interaction among fungi, duff moisture content, and invertebrates. Water-soluble leachates from senescent leaves of madrone have been demonstrated to inhibit germination and lower growth of Douglas-fir seedlings in the laboratory *(3,31)*, a finding not substantiated in the field *(17,31)*.

Early growth of Pacific madrone seedlings is slow. In the Santa Cruz Mountains, shoot and root elongation of 6-month-old seedlings in the sunny environment was 4 cm (2 in) for shoots and 10 cm (4 in) for roots; in the shady environment, 3 cm (1 in) for shoots and 4 cm (2 in) for roots. Two-year-old seedlings in the Sierra Nevada averaged 9 cm (3.5 in) tall.

Death of madrone seedlings from transplanting has been described as distressingly high, but ease of propagation from cuttings as fair.

Vegetative Reproduction—Pacific madrone reproduces mainly by sprouting. Sprouts arise from dormant buds formed at or just above the root collar and tend to be numerous. More than 300 sprouts were counted on a single low 10-inch-diameter Pacific madrone stump in the northern Sierra Nevada.

Low stumps generally produce more sprouts than high stumps. High stumps sometimes support undesirable stool sprouts that form on the edge of the cut surface or, less commonly, on the vertical portion of the stump between the ground and the top. Stool sprouts tend to become infected with heart rot at an early age and are more susceptible to dieback and death than sprouts from the root crown. Stool sprouts that survive seem to grow well, but their longevity is unknown.

Pacific madrone sprouts grow rapidly. On a site of medium quality in the Klamath Mountains, 3-year-old sprout clumps averaged 13 members per clump, 3.1 m (10 ft) in height, and 2.3 m (7.6 ft) in width *(22)*. In the northern Sierra Nevada on a good site, the annual enlargement of sprout clumps was measured in both a clearcut and a shelterwood. After 10 years, sprouts were taller, 6.7 vs 3.0 m (22 vs 10 ft); wider, 3.1 vs 2.1 m (10.1 vs 7.0 ft); contained more sprouts (15 vs 7); and possessed more volume, 52.1 vs 19.8 m³ (1,840 vs 700 ft³) *(12)*. In both locations, annual growth of 1.5 m (5 ft) on 2- to 5-year-old sprouts was observed for particularly vigorous members of a clump. Seven years after cutting and burning in southwest Oregon, dense stands of madrone sprout clumps spaced 2.7 by 2.7 m (9 by 9 ft) had a basal area of about 22 m²/ha (96 ft²/acre), 84 percent cover, and an above-ground biomass of 25,000 kg/ha (22,500 lb/acre) *(9)*. This rapid early growth, both in height and crown width, allows Pacific madrone to dominate conifer and shrub associates for many years. It also means that understory species of grasses, forbs, and shrubs are quickly excluded from madrone sprout stands following disturbance *(9)*. In spite of a leaf canopy that is more open than that of tanoak and giant chinkapin (*Castanopsis chrysophylla*) *(16)*.

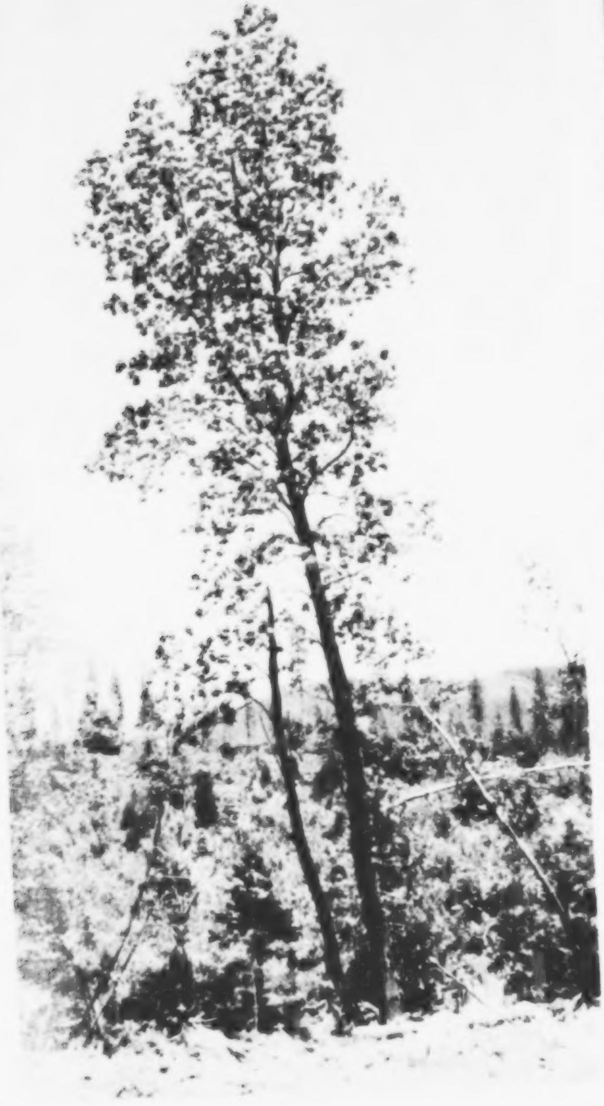
New information is available for forecasting site occupancy of Pacific madrone for up to 6 years after disturbance. It includes equations that relate width and area of sprout clumps originating from trees greater than 1 inch d.b.h. to size of parent stem and time since cutting *(28)*, and equations that predict potential leaf area and biomass by parent tree diameter class *(7)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Most of the Pacific madrone trees observed originate from sprouts (fig. 2), and their growth and form are influenced thereby. Position of the sprout in the clump, for example, often governs form. Members in the center of the clump grow straighter than those on the edge, which tend to lean outward or be J-shaped. In general, trees in the crowded forest have better form and are less branchy than those in the open.

Madrone usually is a stately tree, tall and straight of bole if on good sites in forested canyons and draws (fig. 3). But the species frequently is low and shrubby with multiple stems, if on poor sites, especially on south-facing benches and ridges.

Growth of madrone has been described as slow, especially in diameter *(27)*. In the northern Sierra Nevada on good sites, madrone trees average 5 to 6 rings per centimeter (12 to 15 rings/in) of diameter *(12)*. Here, stand density of mixed hardwoods, which include California black oak and tanoak, as well as



ure 2—*Two members of a Pacific madrone clump, one of which* *d. In a few years, the other will stand alone. It is 25 cm (9.8* *d.b.h. and 14 m (46 ft) tall.*

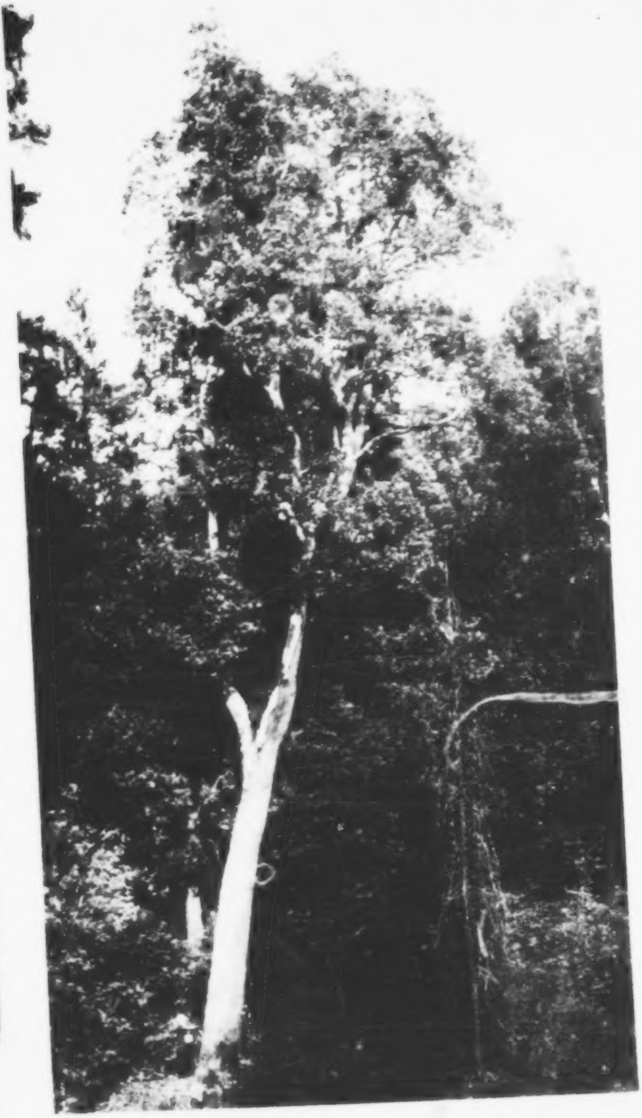


Figure 3—*A Pacific madrone growing near the bottom of a steep canyon on the Plumas National Forest, CA. The tree, 32 m (105 ft) tall and 97 cm (38 in) in d.b.h., dwarfs the man beside it.*

cific madrone, averages 1,630 stems per hectare (659 acre), more than 5 cm (2 in) in d.b.h., and 45.5 2/ha (198 ft2/acre) of basal area. As madrone general- grows in dense stands, this growth rate is probably pical of trees 55 to 65 years of age on similar sites.

The relationship of d.b.h. to total tree height for adrone in the northern Sierra Nevada is curvilinear. Although fitted freehand, the curve indicates that trees 20 cm (8 in) in diameter are about 15 m (49 ft) tall; those 40 cm (16 in), 23 m (75 ft) tall; and trees 60 cm (24 in) in diameter are almost 28 m (92 ft) in height (fig. 4).

When dense stands in the Sierra Nevada were given a crown thinning that reduced basal area by

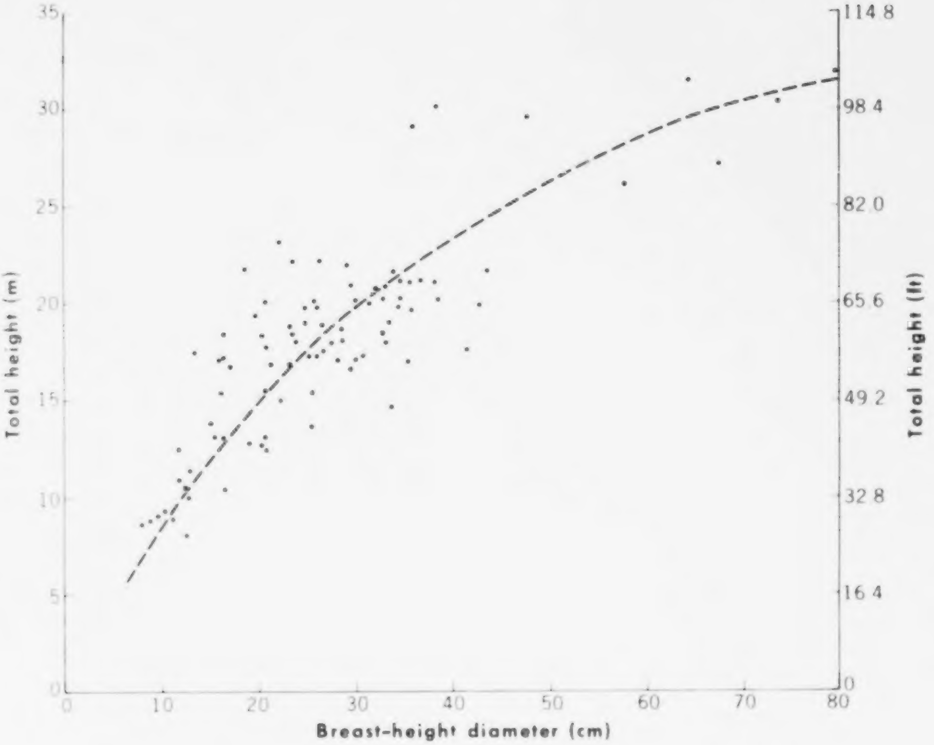


Figure 4—*Diameter-height relationship of Pacific madrone in north-central California*

34 to 55 percent, early analyses showed that diameter growth on thinned plots was more than twice that of the control plot: 23 mm per tree compared to 10 mm (0.9 to 0.4 in) after 8 years. In thinned plots and control, diameter growth of trees was successively better as crown class increased from suppressed to dominant. Preliminary trends indicated that stands thinned below 25.3 m²/ha (110 ft²/acre) of basal area were too open and probably too warm for best diameter growth *(13)*. The higher density level where growth decreased from overcrowding has not been defined.

Although the longevity of madrone is not known, the species has been referred to as "giving evidence of being long lived" *(27)*. Trees 200 to 250 years old have been recorded and large specimens are estimated to be 400 to 500 years old.

Madrone seldom exceeds 34 m (110 ft) in height and 152 cm (60 in) in breast-height diameter. The largest Pacific madrone on record grows in Humboldt County, CA, and is 24 m (79 ft) tall and over 975 cm (384 in) in circumference 0.9 m (3 ft) above ground *(19)*.

Volume per hectare of madrone generally is low because the species seldom grows in pure stands. In the 60-year-old mixed-hardwood stand in the northern Sierra Nevada, Pacific madrone constituted nearly 16 percent of total stand volume of 44.7 m³/ha (638 ft³/acre).

Rooting Habit—Two- to 5-year-old madrone seedlings, growing in partial shade, showed large variation in root pattern and length. Some seedlings had a curving, twisting primary root with moderately extensive lateral development, and others had moderately twisted primary roots just below groundline that straightened and grew downward for about 23 cm (9 in).

Trees 50 to 60 years old often have a well-developed root burl from which a spreading root system develops. Some of these roots extend into organi layers near the soil surface and others slan downward. Large trees, 61 to 91 cm (24 to 36 in) i d.b.h., can produce massive root burls 122 to 152 c (48 to 60 in) in diameter. Uprooted trees indicate system composed of deep, spreading lateral roots.

Reaction to Competition—Young Pacifi madrone seedlings need partial shade for estab lishment, especially in the southern portion of their range. As trees age, the need for light increases and older trees require top light for survival. In British Columbia, the species has a low shade tolerance. An appropriate overall classification for the species is intermediate in tolerance to shade. Pacific madrone probably is more subclimax than climax in successional status.

Damaging Agents—Fire is a major damaging agent to thin-barked madrone. Even the thicker bark at the base of old trees shields them little. Seedlings, sprouts, and trees all die back to the root crown after fire but rarely are killed. Competing conifers usually are damaged badly or killed, however, allowing the fast-growing madrone sprouts to establish dominance.

Animal damage to Pacific madrone is minor. Deer eat berries and browse tender shoots of low crowns and young trees.

Insect damage is minor, and not economically significant. Several types of insects cause minor damage, including defoliators, leaf miners, wood borers, and bark beetles *(5)*. One of the most commonly observed types of damage on madrone leaves is the sinuous track of the larva of *Marmara arbutella*. Damage, however, is relatively minor. The fall webworm *(Hyphantria cunea)* commonly deforms young trees and sprouts.

The pathology of Pacific madrone is characterized by many leaf spots, one leaf rust, a spot anthracnose, a tar spot, at least four cankers, and a root disease. A major cause of dieback and death of Pacific madrone is *Fusicoccum aesculi* (asexual stage), *Botryosphaeria dothidea* (sexual stage), which presently is virulent in northern California. This fungus disease, known as "madrone canker," begins on branch tips and moves inward. Symptoms of the disease are a dieback of branch tips followed by a dark wine-red discoloration of the bark that turns black after the branch dies. Continued advance of the infection leads to a wedge-shaped canker that eventually encircles and kills the branch. The blackened surface of the dead branch looks like fire damage. Cankered areas often spread from branches to bole and expand into the heartwood of the tree. Twigs, branches, and whole trees can be killed by this canker. Occasionally, branch dieback stops at a node. Sometimes several members of a sprout clump die back and sometimes all the sprouts in a clump succumb. Spores produced in the outer bark are probably spread by rain and wind, and also by insects *(10)*. The disease probably was widespread and causing insignificant damage in forest stands, but has become a serious problem over the past 10-12 years. Changing environmental conditions are thought to have encouraged the outbreak of this disease. This pest has been reported as damaging Pacific madrone in the northern half of its range in California and has been observed in Oregon and Washington. The common twig fungus *(Botryosphaeria ribis)* infects madrone but is not common. A serious disease of madrone is a canker *(Phytophthora cactorum)* that can affect its culture in occasional situations. Cankers of this species appear to originate at ground-line and spread up the bole for an unknown distance. Early symptoms are browning and death of new leaves and a thinning of the crown. By the time these symptoms are obvious, extensive basal cankering usually has taken place *(8)*. Another canker *(Hendersonula toruloidea)* is fairly widespread on madrone in British Columbia. Annosus root rot *(Heterobasidion annosum)*, which killed more than 100 trees in Amador County, CA, in 1976, is a pest of high potential damage *(1)*.

Several species of fungi cause serious damage to the heartwood of madrone trees. The most important are *Phellinus igniarius*, *Fomitopsis cajanderi* *(Fomes subroseus)*, and *Poria subacida*. In the mixed conifer-hardwood forest of northwestern California, living madrones with fungus-infected heartwood are heavily utilized by cavity-nesting birds *(21)*.

Special Uses

Wood of Pacific madrone is moderately dense and strong, and extremely hard. When dry, its color, grain, and figure resemble that of black cherry. It is especially handsome in rotary-cut veneer *(18)*. The wood is well suited for use as bobbins, shuttles, novelties, and tobacco pipes and is recommended for furniture, paneling, flooring, interior trim, charcoal, and odor-free food-storage units *(32)*. Early Californians preferred madrone charcoal over that from other species for manufacturing gunpowder.

Nearly all of the products mentioned have been manufactured in the past. Current utilization is for some of these products as well as fuelwood.

The smooth reddish-orange bark of trunk and limbs, shiny green leaves, and colorful berries have led to use of madrone as an ornamental.

Genetics

Other than possible horticultural varieties, no natural varieties or hybrids are known.

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Betula alleghaniensis Britton   Yellow Birch

Betulaceae   Birch family

G. G. Erdmann

Yellow birch (*Betula alleghaniensis*) is the most valuable of the native birches. It is easily recognized by the yellowish-bronze exfoliating bark for which it is named. The inner bark is aromatic and has a flavor of wintergreen. Other names are gray birch, silver birch, and swamp birch. This slow-growing long-lived tree is found with other hardwoods and conifers on moist well-drained soils of the uplands and mountain ravines. It is an important source of hardwood lumber and a good browse plant for deer and moose. Other wildlife feed on the buds and seeds.

Habitat

Native Range

Yellow birch (fig. 1) ranges from Newfoundland, Nova Scotia, New Brunswick, and Anticosti Island west through southern Ontario to extreme southeastern Manitoba; south to Minnesota and northeastern Iowa; east to northern Illinois, Ohio, Pennsylvania to northern New Jersey and New England; and south in the Appalachian Mountains to eastern Tennessee and northeastern Georgia. Southward yellow birch grows at higher elevations, appears more sporadically, and finally is restricted to moist gorges above 914 m (3,000 ft).

The largest concentrations of yellow birch timber are found in Quebec, Ontario, Maine, Upper Michigan, New York, and New Brunswick (*96*). About 50 percent of the growing stock volume of yellow birch in North America is in Quebec.

Climate

Yellow birch grows in cool areas with abundant precipitation. Its northern limit coincides with the 2° C (35° F) average annual temperature isotherm, and its southern and western limits coincide with the 30° C (86° F) maximum temperature isotherm (*31*). Although the average annual temperature is about 7° C (45° F) throughout its range, temperature extremes range from -40° C to 38° C (-40° F to 100° F) (*45*). Annual precipitation ranges from about 1270 mm (50 in) in the East to 640 mm (25 in) in central Minnesota at its western limit. More than half of the precipitation may be snow. Snowfall ranges from 152 to 356 cm (60 to 140 in) and averages 229 cm (90 in) in the north. The growing season ranges from 60 to 150 days and averages about 120 days.

Soils and Topography

Yellow birch grows over a large area with diverse geology, topography, and soil and moisture conditions. In Michigan and Wisconsin it is found on glacial tills, outwash sands, lacustrine deposits, shallow loess deposits, and residual soils derived from sandstone, limestone, and igneous and metamorphic rock (*95*). Soils are also derived from granites, schists, and shales in other parts of its range.

Growth of yellow birch is affected by soil texture, drainage, rooting depth, stone content in the rooting zone, elevation, aspect, and fertility. Yellow birch grows best on well-drained, fertile loams and moderately well-drained sandy loams within the soil orders Spodosols and Inceptisols and on flats and lower slopes (*45*). It also grows on Alfisols typical of the humid temperature forest region. Rootlet development is profuse in loam but poor in sand. Even though its growth is poor, yellow birch is often abundant where drainage is restricted because competition from other species is less severe.

In the Lake States birch grows best on well- and moderately well-drained soils and on lacustrine soils capped with loess. Its growth is poor on poorly-drained lacustrine soils, shallow soils over limestone, and coarse-textured sandy loams without profile development (*95*). Site quality between the best and poorest sites differs by more than 9 m (30 ft) at 50 years.

In the Green Mountains of Vermont birch grows on unstratified glacial till up to 792 m (2,600 ft) (*109*). Here, thickness of the upper soil horizon as influenced by elevation and aspect have been used to estimate site index—birch grows better at lower elevations than higher elevations and on northeast aspects than southwest aspects.

Associated Forest Cover

Yellow birch is present in all stages of forest succession. Second-growth stands contain about the same proportion (12 percent) of birch as virgin stands. Yellow birch is usually found singly or in small pure groups in mixtures with other species.

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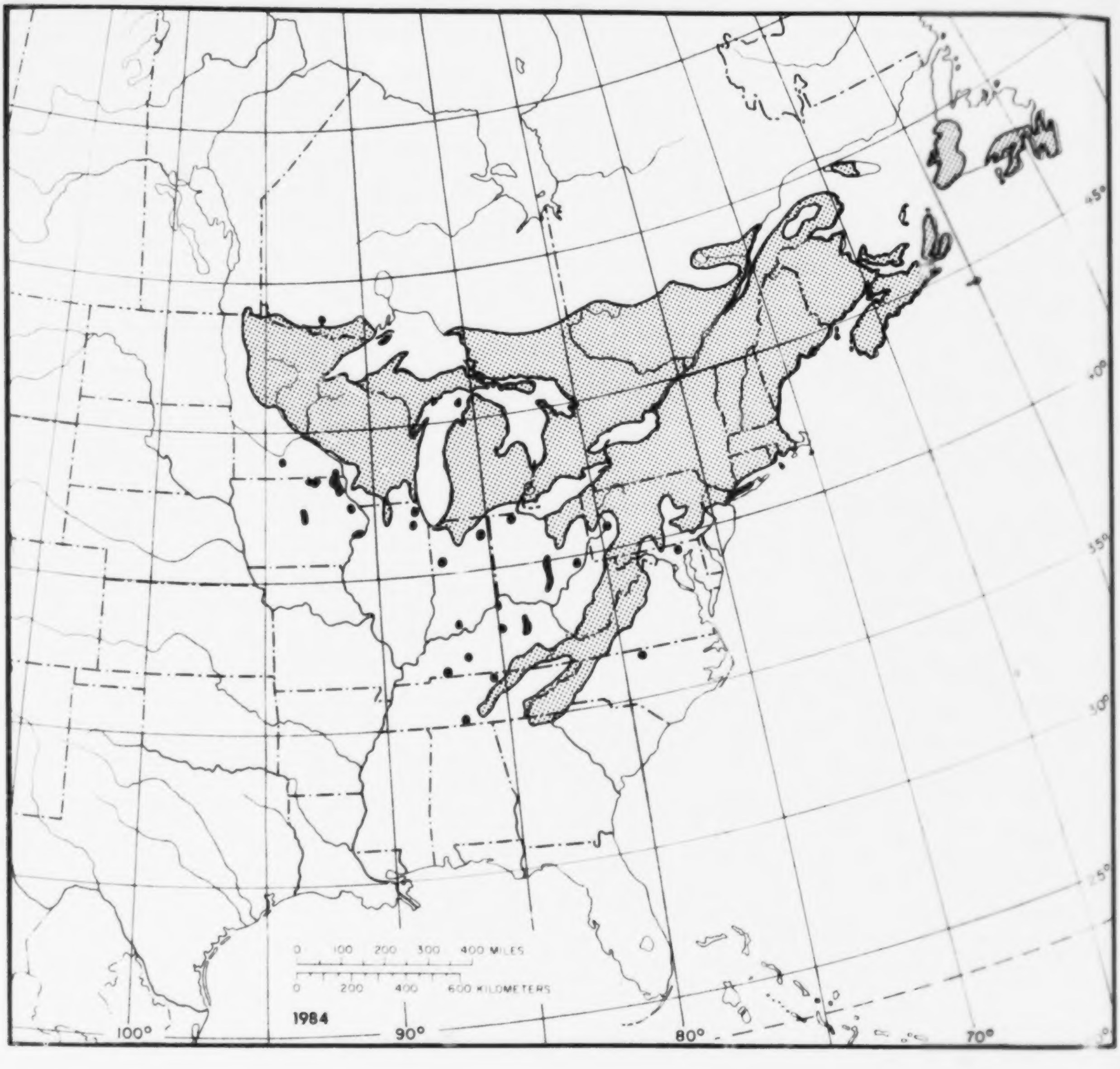

Figure 1—*The native range of yellow birch.*

Because yellow birch is seldom found in pure stands, it is not recognized as a separate type.

Yellow birch is a major component of three forest cover types: Hemlock–Yellow Birch (Society of American Foresters Type 24), Sugar Maple–Beech–Yellow Birch (Type 25), and Red Spruce–Yellow Birch (Type 30) *(41)*. Hemlock–Yellow Birch is considered a long-lasting subclimax type, as is Red Spruce–Yellow Birch, except on moist sites, where it is a climax type *(74)*.

Yellow birch is a commonly associated species in the following forest cover types *(41)*: Balsam Fir (Type 5), Pin Cherry (Type 17), Paper Birch (Type 18), Gray Birch–Red Maple (Type 19), White Pine–Northern Red Oak–Red Maple (Type 20), Eastern White Pine (Type 21), White Pine–Hemlock (Type

22), Eastern Hemlock (Type 23), Sugar Maple–Basswood (Type 26), Sugar Maple (Type 27), Black Cherry (Type 28), Red Spruce–Sugar Maple–Beech (Type 31), Red Spruce (Type 32), Red Spruce–Balsam Fir (Type 33), Red Spruce–Fraser Fir (Type 34), Paper Birch–Red Spruce–Balsam Fir (Type 35), Northern White-Cedar (Type 37), Black Ash–American Elm–Red Maple (Type 39), Yellow-Poplar (Type 57), Yellow-Poplar–Eastern Hemlock (Type 58), Yellow-Poplar–White Oak–Northern Red Oak (Type 59), Beech–Sugar Maple (Type 60), White Spruce (Type 107), and Red Maple (Type 108).

Yellow birch commonly grows in stands with sweet birch (*Betula lenta*), eastern hophornbeam (*Ostrya virginiana*), American hornbeam (*Carpinus caroliniana*), and as an understory tree in Aspen (Type 16). Small trees and shrubs commonly associated with yellow birch in the north are striped maple (*Acer pensylvanicum*), mountain maple (*A. spicatum*), alternate-leaf dogwood (*Cornus alternifolia*), beaked hazel (*Corylus cornuta*), Atlantic leatherwood (*Dirca palustris*), witch-hazel (*Hamamelis virginiana*), fly honeysuckle (*Lonicera canadensis*), American mountain-ash (*Sorbus americana*), American elder (*Sambucus canadensis*), Canada yew (*Taxus canadensis*), mapleleaf viburnum (*Viburnum acerifolium*), hobblebush (*V. alnifolium*). Between cliffs of deep, narrow gorges and upper coves of the southern Appalachians, yellow birch is frequently associated with three evergreen shrubs—American holly (*Ilex opaca*), drooping leucothoe (*Leucothoe catesbaei*), and rosebay rhododendron (*Rhododendron maximum*)—and with striped maple, sassafras (*Sassafras albidum*), and mapleleaf viburnum.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yellow birch is monoecious; male and female catkins are borne separately on the same branch. Erect staminate catkins are formed during late summer in clusters of two or three, or singly at the tips of long shoots. Individual florets of a staminate catkin contain three flowers and each flower has three bilocular anthers. The greenish staminate catkins, 6 cm (2.2 in) long, remain on the tree over winter. In the spring they turn purplish yellow while elongating to 7 to 10 cm (2.8 to 3.9 in) and then shed pollen for 3 to 5 days. Solitary pistillate catkins also formed during the fall are enclosed in buds over winter; they appear terminally as greenish catkins (each about 2 cm or 0.8 in) on short branchlets with the leaves in late May to early June. Each floret contains three naked flowers and is subtended by a three-lobed bract. Each flower consists of a bicarpellary ovary with two styles. Female flowers are receptive from 2 to 5 days before pollen is shed on the same tree (*29*). Normally only one of the two ovules in each chamber develops into a seed; the other three abort. Occasionally both ovules within one ovary are fertilized and two seedlings emerge from one seed (*17*).

The fruit, a winged nutlet, ripens in late August or early September. Each nutlet averages from 3.2 to 3.5 mm (0.13 to 0.14 in) long without the wings. Mature seeds have light brown or tan seed coats and firm white interiors.

Seed Production and Dissemination—Normally, 40 years is considered the minimum and 70 years the optimum seed-bearing age for yellow birch (*45*), but heavy seed crops are also produced by 30- to 40-year-old trees in either open-grown positions or thinned stands. However, open-grown progeny test saplings with large crowns bear viable seed at 7 years and male catkins at 8 years (*21*). Germinable seed has also been obtained from 16-year-old trees 5 to 10 cm (2 to 4 in) in d.b.h. and 6.7 to 7.6 m (22 to 25 ft) tall.

Good seed crops usually occur at about 2 to 3 year intervals but the frequency of good or better seed crops varies—every 1 to 4 years in northeastern Wisconsin (*47*), and every 2 to 3 years in Maine, and every 3 years in Ontario (*10*). Consecutive good or better seed crops only occurred once in the 26-year Wisconsin study; 60 percent of the intervening crops failed or were poor. Seed-crop failures are often caused by hard frost in late spring or early fall or by insects and disease. The percentage of viable seeds produced varies each year and can be very low due to a high proportion of seedcoats without embryos, probably caused by parthenocarpy (*14*). Seed viability is often affected by weather conditions during pollination, fertilization, and seed development. It also varies by locality, stand, and individual trees within the same stand.

Although some seeds fall shortly after they mature in August, the first heavy seedfall in Canada and the northern United States comes with cold weather in October. Contrary to earlier reports, larger seeds are not shed first nor is their germination capacity any better than that of smaller filled seeds (*17*).

Yellow birch seeds are light, averaging 99,200/kg (45,000/lb) (*8*). They are dispersed by the wind and blown up to 400 m (1,320 ft) over crusted snow (*10*). Dispersal of adequate amounts for regeneration is at least 100 m (330 ft) from the edge of a fully stocked mature northern hardwood stand.

Yellow birch is a prolific seeder, producing between 2.5 and 12.4 million seeds per hectare (1 to 5 million/acre) in good seed years *(45)*, and up to 89 million/ha (36 million/acre) in a bumper seed year *(52)*. Seed viability is usually good in years with heavy seed crops and poor in years with light crops. Germinative capacity in good seed years is still low, however, averaging about 20 percent under natural conditions.

The next seed crop can be estimated from the abundance of the overwintering male catkins *(88)*. Fairly reliable estimates of the fall yellow birch seed crop can also be obtained from the size of the spring-maturing red maple crop *(47)*.

Yellow birch seedcoats contain a water-soluble germination inhibitor that is inactivated by light *(17)*. Seed dormancy can be broken down artificially either by stratifying the seed in moist peat or sand at 5° C (41° F) for 4 to 8 weeks or by germinating unchilled seeds in a water medium under "cool-white" fluorescent light for more than 20 days. Germination test results are always higher when unchilled rather than stratified seeds are used *(8)*. Following stratification, seeds are germinated at alternating day and night temperatures of 32° C and 15° C (90° F and 59° F) for 30 to 40 days, and alternating temperature of 30° C and 20° C (86° F and 68° F) with at least 8-hour light periods are used for unchilled seeds. Germination percentages exceeding 90 percent are common in good seed years.

Seeds can be stored in tightly closed bottles at from 2 to 4° C (36 to 40° F) for 4 years without losing viability *(17)*. Some seed lots stored well for 8 years and one lot still had 65 percent germination after 12 years *(19)*.

Seedling Development—Yellow birch seeds dispersed in the fall and winter germinate at warm temperatures in early June. Germination is epigeal. In undisturbed stands, yellow birch can only regenerate on mossy logs, decayed wood, rotten stumps, cracks in boulders, and windthrown hummocks because hardwood leaf litter is detrimental to its survival elsewhere *(45)*. In June most seeds germinate in compacted leaf litter that birch radicals and hypocotyls cannot pierce *(10)*. Drying of the litter during the growing season kills most germinants. The remaining seedlings later succumb to frost damage or are smothered by the next leaf fall.

Unless stands have been burned or heavily disturbed by blowdowns or logging, abundant birch regeneration is normally restricted to edges of skidroads or landing areas on well-drained sites. On less-well-drained soils, sufficient moisture remains in the leaf litter to result in adequate establishment if advance regeneration of other species is removed *(117)*.

The most important factors affecting the catch of yellow birch seedlings are an adequate seed supply, favorable weather, proper seedbed conditions, adequate light, and control of competition.

Removing advance regeneration is at least as important as preparing proper seedbeds *(121)*. Scarification fulfills both requirements and, when coupled with opening of the canopy, can greatly increase the initial catch of birch seedlings *(45)*. Optimum seedling survival and growth, however, occur on disturbed humus or mixed humus mineral soil seedbeds in the absence of advance regeneration *(126)*.

Mechanical scarification and prescribed burning are used to prepare receptive seedbeds and eliminate advance regeneration. Scarification should be shallow to mix humus and mineral soil and to expose 50 to 75 percent of the area *(46,88)*. Spring burning during and shortly after leafout in years with abundant male birch catkins may also control competition from advanced regeneration and provide seed for successful birch regeneration. Treatments should coincide with good seed crops because the effects of scarification are largely lost after two or three growing seasons.

Under dense forest canopies (13 and 15 percent of full sunlight) yellow birch roots grow slower than sugar maple seedlings *(81)*. As a result, few yellow birch become established under selection cutting *(43)*.

The optimum light level for top growth and root development of birch seedlings up to 5 years old is 45 to 50 percent of full sunlight *(43)*. The best root-to-shoot ratios are also produced at similar light levels *(86)*. In field studies, the greatest 2-year height growth occurred at the lowest canopy density of 0 to 14 percent, and on mixed humus and mineral soil seedbeds it occurred under canopy densities between 29 and 50 percent *(123)*. Moderate side shade is beneficial to birch seedlings during their first 5 years *(124)*.

Clearcutting small patches or strips provides suitable conditions for yellow birch seedling establishment in the Northeast where rainfall is abundant. Scarified clearcut patches of 0.04 to 0.24 ha (0.1 to 0.6 acre) produce good catches of birch regeneration. Patches are difficult to manage but can be used in uneven-aged management to increase the proportion of birch *(43)* when groups of mature or defective trees are harvested *(85)*.

In the dry western part of the species range, success with strip clearcutting to regenerate birch has been too variable to generally recommend its use. In

Upper Michigan success depends on a good seed crop, favorable weather, and control of advance regeneration *(89)*. Although strips 20 and 40 m (66 and 132 ft) wide were equally well stocked with birch seedlings after 6 or 7 years in Michigan, strips 20 m (66 ft) wide are about optimum in Canada *(10)*, and strips 15 m (50 ft) wide are recommended in the Northeast *(43)*.

Clearcuttings of 2 to 4 ha (5 to 10 acres) and uniform selection cuttings are not as effective as smaller patches or the shelterwood method for establishing yellow birch stands *(87,90)*. In the western part of its range, birch regenerates best under shelterwood cuttings *(48,121)*. Ten well-distributed yellow birch seed trees per hectare (4/acre) provide an adequate seed supply *(88)*. Otherwise, 0.56 kg/ha (0.5 lb/acre) of stratified (6 to 8 weeks at 5° C (41° C) birch seed can be applied about a week after site preparation in May *(46)* or unstratified seed can be sown before January *(48)*.

Yellow birch can also be successfully established by planting 2-0 stock 15 to 50 cm (6 to 20 in) tall on 0.08 ha (0.2 acre) clearcut patches *(97)*.

Yellow birch seedling growth in the Northeast is limited by inadequate soil fertility in acid sandy subsoils and can be greatly improved by deep fertilizing with phosphorus and lime to correct phosphorus deficiency and aluminum toxicity *(61)*. Aluminum is toxic to roots, especially in subsoils, deficient in magnesium and sulfur. Seedling roots are tolerant of aluminum concentrations or up to 80 p/m but concentration of 120 p/m or more are toxic *(84)*.

Manganese toxicity in seedlings occurs above foliar concentrations of more than 1,300 p/m; concentrations of less than 60 p/m are deficient; and 440 p/m are optimum *(64)*.

Optimum nursery seedbed density is about 160 seedlings per square meter (15/ft^2) *(45)*. Normally 2-0 stock averaging 28 cm (11 in) tall with roots 23 cm (9 in) long and 5 mm (0.2 in) in stem caliper is large enough for dormant spring planting. For early starts in the greenhouse, seedlings require at least 2 months of cold storage to break dormancy *(34)*. Containerized planting is feasible *(11,50,115)*. In 3 months seedlings 40 to 50 cm (16 to 20 in) tall can be produced in the greenhouse using 20-hour days with supplemental cool-white fluorescent and incandescent light *(17)*. Growth can also be accelerated by using plastic greenhouses *(94)*.

After 5 years, yellow birch seedlings are normally overtopped by faster-growing species and require complete release from overstory shading for best survival, growth, and quality development. Photosynthetic rates of overtopped seedlings are only 54 to 70 percent of those grown in full sunlight and their dry weights are 66 percent lower *(82)*.

Birch crop trees in Vermont and Michigan seedling stands (up to 2.5 cm or 1 in d.b.h.) have benefited from cleaning or early release *(40,55)*. After 9 years, trees cleaned to within a 2.4 m (8 ft) radius of the bole radius in Michigan exhibited the best stem, crown, and branch characteristics. They averaged 2 cm (0.8 in) larger in d.b.h. and 0.5 m (1.6 ft) taller than the control trees. Shoot growth of yellow birch partly depends upon current photosynthate *(73)*. The shoot elongation period for released saplings (1.5-m or 5-ft radius) can be extended up to 30 days by making more light and moisture available to them *(55)*.

Vegetative Reproduction—Yellow birch seedlings and small saplings reproduce from sprouts when cut, but sprouting from larger stems is very poor *(93,111)*.

Greenwood cuttings of birch have been successfully rooted *(45)* and overwintered *(56)*. The species can also be propagated by grafting *(17)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Yellow birch (fig. 2) requires overhead light, crown expansion space, soil moisture, and nutrients to compete with its faster growing associates. Crop tree release studies in saplings *(39,54,55,57)*, poles *(36)*, and small saw logs *(37)* in the Lake States and the Northeast demonstrate that 16- to 65-year-old trees respond well to release and can maintain themselves in favorable growing positions throughout their lives. Growth rates, however, gradually decline as trees age.

In the sapling stage, growth rates can be increased up to 8 cm (3 in) per decade by release of dominant and codominant crop tree crowns from all trees whose crowns are within 1.8 to 2.4 m (6 to 8 ft) of the crop trees' crown perimeters *(39)*.

Diameter growth rates of pole-size trees can be increased from 75 to 78 percent by providing the same open growing space between tree crowns as for saplings *(36)*. Dominant and codominant crop trees with well-developed crowns respond best to release. Complete crown release provides adequate crown and root expansion space for optimizing growth rate and quality development in yellow birch. In practice no more than 247 well-spaced crop trees (6.4 m or 21 ft apart) per hectare (100/acre) are released to produce 150 final harvest trees 46 cm or 18 in d.b.h. per hectare (61/acre).

Diameter growth rates of saw log-size trees can also be increased by about 45 percent by either removing two important crown competitors or providing 1.5 m (5 ft) of crown expansion space *(37)*. Through careful tending with even-aged management techniques, trees 46 cm (18 in) in d.b.h. can be produced in less than 90 years.

Even-aged and uneven-aged stocking guides for northern hardwoods have been developed for mixed stands in the Lake States *(40,119)* and the Northeast *(79,113)*. For even-aged stands these guides suggest leaving a residual stand of 60 to 80 percent of full stocking and retaining increasing amounts of basal areas as stands mature. Only small yields of birch proportional to the amounts of birch saw log volumes are obtained from selectively cut stands. Growth rates and yields from mixed softwood stands are higher *(45)*. The most promising trees for future grade improvement should be left after thinning or crown release. Yellow birch trees are financially mature at 56 cm (22 in) in d.b.h. but the maximum d.b.h. may be 46 cm (18 in) where surface defects prevent improvement to top-grade saw or veneer logs *(78)*.

Yellow birch prunes itself well as long as its crown is allowed to close within 5 or 6 years after release. It can, however, be pruned to 50 percent of its height without reducing growth. Pruning should be done on small, fast-growing trees with small knotty cores to limit discoloration and keep decay organisms from entering wounds *(114)*. Branches up to 5 cm (2 in) in diameter can be pruned flush without causing lumber defects. Most wounds up to 5 cm (2 in) close within 7 years *(112)*.

Yellow birch trees are sensitive to excessive exposure following heavy cutting and commonly develop epicormic branches from dormant buds. Intermediate and suppressed trees feather out more than dominant and codominant trees. Epicormic sprouting increases with intensity of release but is not a serious problem in managed stands where periodic thinnings follow crown closure *(36)*. Sprouting is usually more profuse just beneath the live crown than further down the stem.

In 60- and 80-year-old New Hampshire stands, addition of nitrogen, phosphorus, calcium, and magnesium to the acid subsoil of Spodosols and large dolomitic limestone applications were suggested for alleviating these deficiencies in yellow birch and for correcting aluminum toxicity in the roots and high manganese levels in the leaves *(62,63)*. Zinc application is a more economical way to correct calcium deficiency of stems and leaves and aluminum toxicity of roots *(65)*.

Six percent and 51 percent increases in average 8-year basal area growth of 90-year-old trees have been reported from applications of lime and lime plus nitrogen, phosphorus, and potassium, respectively *(98)*. Lime increased crown-sectional area growth of 70-year-old thinned trees in New York 1 year after broadcast application, by making more calcium and magnesium available for uptake *(77)*.

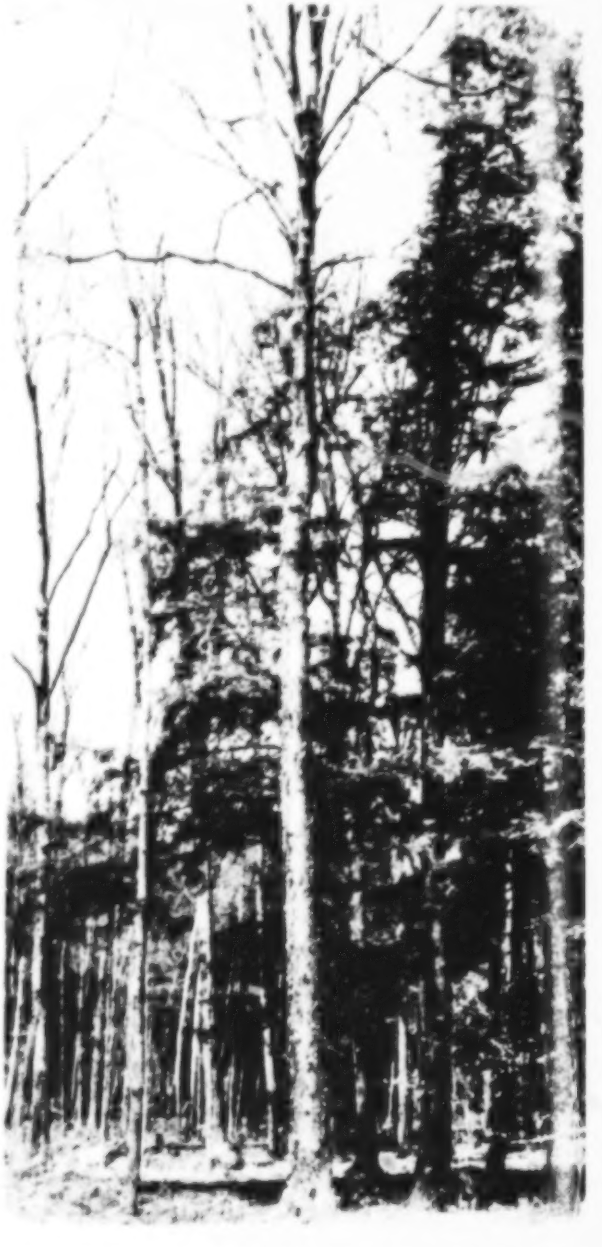

Figure 2—*A mature yellow birch tree, 46 cm (18 in) in d.b.h. in Wisconsin.*

Lake States fertilizer studies in a 65-year-old sawtimber stand and two pole-size stands showed no significant diameter growth responses to varying amounts and combinations of nitrogen, phosphorus, and potassium broadcast fertilizer applications that occurred within 3 years of treatment *(37,116)*.

Yellow birch is one of the slowest growing components of both old growth and unmanaged second growth northern hardwood forests. D.b.h. growth rates of less than 2.5 cm (1 in) in 10 years are common in unmanaged stands or stands managed under the uneven-aged system. Fifteen-year mortality exceeded ingrowth for birch in selectively cut 45-year-old stands in Wisconsin *(35)*.

Complete tree and component part biomass equations have been published for yellow birch trees from 0.25 to 66 cm (0.1 to 26 in) in d.b.h. and seedlings 0.3 to 1.2 m (1 to 4 ft) tall in Maine *(128)* and in New Brunswick *(69)*.

Site index curves from stem analysis data have been developed for yellow birch growing in northern hardwood stands in northern Wisconsin and Upper Michigan *(12)* and Vermont *(26)*.

The Vermont curves, when corrected, are also applicable in New Hampshire *(110)*. In northern Wisconsin and Upper Michigan yellow birch grows on a narrow range of site indexes *(13)*. Yellow birch, sugar maple, and red maple have similar site indexes up to age 50 on well-drained soils. On less well-drained soils, yellow birch site index is higher than that of sugar maple. In the Lake States and New England, average site index is about 16.8 to 19.8 m (55 to 65 ft) for birch at age 50. Until age 50 height growth is faster in the Northeast than in the Lake States; after age 50 these height growth patterns are reversed.

In New England mature trees on medium sites have attained a height of up to 30.5 m (100 ft) and a d.b.h. of more than 76 cm (30 in) at age 200 *(45)*. Maturity is normally reached in 120 to 150 years in unmanaged forests *(9)*. The largest specimen on record, near Gould City, MI, is 144 cm (56.7 in) in d.b.h. and 34.7 m (114 ft) tall, with a 30.8 m (101 ft) crown spread. Its cochampion, near Big Bay, MI, is 151 cm (59.5 in) in d.b.h. and 32.6 m (107 ft) tall with a 26.2 m (86 ft) crown spread *(58)*. Yellow birch trees are commonly more than 300 years old and occasionally reach ages of more than 366 years.

Rooting Habit—Yellow birch has an adaptable well-developed, extensive lateral root system. Its roots are capable of either spreading horizontally through shallow soils or penetrating to depths of more than 1.5 m (5 ft) under favorable conditions. Roots often follow old root channels in compacted soil layers. Rooting patterns of older trees in unmanaged stands may be modified by their origin on decayed wood and stumps (fig. 3). Within- and between-tree root grafting is common in birch *(42)*.

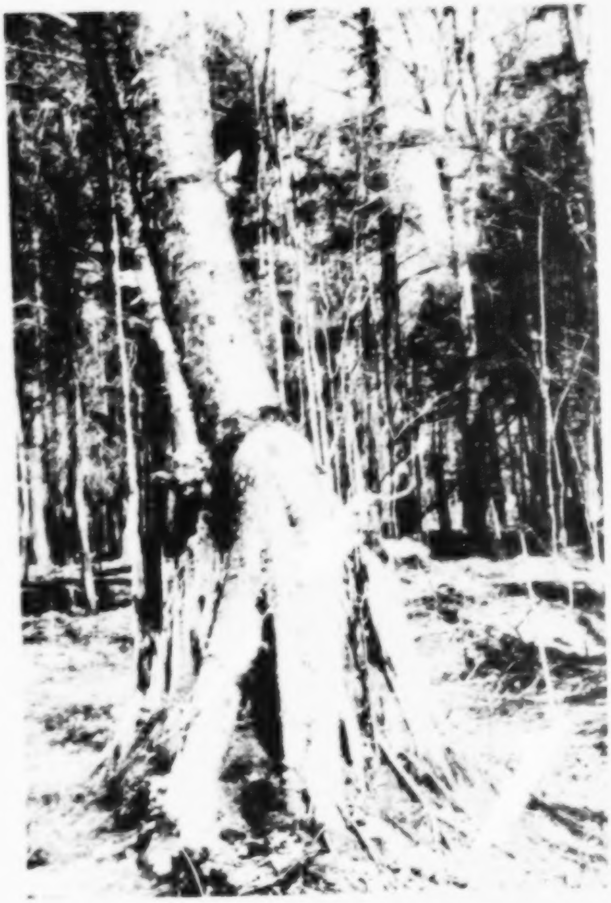

Figure 3—*Stilt-rooted yellow birch, 23 cm (9 in) in d.b.h., that developed on a rotten stump in an unmanaged stand in Wisconsin*

Irregularly distributed lateral roots of sapling and pole-size trees often extend well beyond their crown perimeters *(120)*. Most root systems have irregular circular or oval shapes. Roots of trees on slopes are usually concentrated along the contour and the uphill side of the stem. Main laterals are close to the soil surface and usually have one or two sinker roots within 1.8 m (6 ft) of the stem. These sinkers often penetrate to impervious layers *(53)*. Replacement root growth is active from leafout (May 5) until late October in southern New Hampshire *(99)*.

Reaction to Competition—Yellow birch is generally considered intermediate in shade tolerance and competitive ability *(45)*. It is more shade tolerant than the other native birches, but less tolerant than its major associates, sugar maple *(Acer saccharum)*, beech *(Fagus grandifolia)*, and hemlock *(Tsuga)*. Yellow birch is the major gap-phase component of the forest cover types Sugar Maple– Beech–Yellow Birch and Hemlock–Yellow Birch. It cannot regenerate under a closed canopy; it must have soil disturbance and an opening in the canopy *(125)*. It tends to be stable on moist sites but gives way with age to more tolerant species on dry sites.

Yellow birch is often a pioneer species following fires but is usually less abundant than aspen *(Populus)*, pin cherry *(Prunus pensylvanica)*, and paper birch *(Betula papyrifera)*. Birch seedlings cannot compete successfully with advance regeneration, grass, and herbaceous plants. An allelopathic relation between yellow birch and sugar maple seedlings has been noted *(118)*. Advance sugar maple regeneration offers the stiffest competition in the Sugar Maple–Beech–Yellow Birch cover type, while red maple *(Acer rubrum)* sprouts are the most serious problem on wetter sites in the Lake States.

Damaging Agents—Yellow birch is a very sensitive species that is more susceptible to injury than its common associates. It is windfirm on deep, well-drained loam and sandy loam soils but is subject to windthrow on shallow, somewhat poorly drained soils. Thin-barked yellow birch is susceptible to fire injury. Seedlings and saplings are killed outright by even light surface fires. The fine branching habit of yellow birch makes it susceptible to damage from accumulating ice or snow loads. Large trees are frost hardy *(91)* but late spring frost can kill 10-year-old seedlings, especially on litter seedbeds under full and partial shade. Winter sunscald can be a problem on the south and southwest sides of birch boles. Birch foliage and twigs are injured by wind-borne salt spray. Seed germination is also greatly reduced by 0.20-percent salt concentrations in the soil *(6)*. Simulated acid rain at pH values from 3 up to 4 stimulated birch germination *(80)* but foliar damage occurs at pH levels of 3 or less and seedling growth reductions at pH 2.3 *(127)*. Yellow birch seedlings are tolerant to atmospheric pollution of ozone at 0.25 p/m *(67)* and sensitive to 3.5 p/m of sulfur dioxide *(66)*.

Post-logging decadence is a localized decline from which most trees recover. It consists of top dying and some mortality following heavy cutting in mature and overmature stands. Yellow birch is more susceptible to root, stem, or crown injury and more severely affected than its common hardwood associates. Weakened trees are often attacked and eventually killed by the bronze birch borer.

A decline of yellow birch and paper birch trees, called birch dieback, caused widespread mortality between 1932 and 1955 in eastern Canada and northeast United States. It affected yellow birches of all sizes, even in undisturbed virgin stands. The first visible symptoms of dieback are similar to those of decadence. Foliage in the upper crown appears small, curled, cupped, yellowish, and thin. Following this, tips of branches die, then dying progresses downward, involving entire branches and often more than half the crown within 2 or 3 years. Trees are usually killed within 3 to 5 years by the bronze birch borer, which with root rot fungi, the gold ring spot virus, and other pests have been considered secondary agents associated with birch dieback. Many researchers have attributed birch dieback to adverse climatic conditions, drought, and increased soil temperature, over an extended period, which caused rootlet mortality that weakened the trees and predisposed them to attacks by the borer. Others have considered overmaturity, past cutting practices, killing of associated trees by disease and the spruce budworm, and defoliating insect outbreaks on birch as initially responsible for weakening the trees. More recently the apple mosaic virus *(49)* and the "frozen soil" theory *(59)* have been suggested as the possible triggering mechanisms for birch dieback. Under the "frozen soil" theory, shallow-rooted birch trees in years without snow cover are apparently unable to replace moisture losses from their stems through both frozen rootlets and those broken from frost heaving. To date, no single "triggering" cause of birch dieback has been widely accepted, but the condition is probably the result of one or more of the indicated stress factors.

Top-dying and reduced growth of yellow birch crowns have also been associated with heavy birch seed crops *(51)*. This dieback occurs the year after bumper seed crops and is limited to the peripheral 0.6 to 0.9 m (2 to 3 ft) of branch tips on mature trees and usually just the past season's growth on younger trees.

Discoloration and decay are the major causes of defect and loss in wood quality of yellow birch *(75,92)*. Discoloration and decay develop more rapidly in yellow birch than other diffuse-porous northern hardwood species *(60,107)*. Some of the nonhymenomycetes most frequently isolated from discolored wood associated with birch wounds are *Libertella betulina, Trichocladium canadense, Phialophora* spp., *Phialocephala* spp., *Hypoxylon* spp., and *Nectria* spp. *(32,103,104,107)*.

Mechnical wounds with more than 320 cm^2 (50 in^2) of exposed wood are important entrance courts for decay fungi *(92)*. *Pholiota limonella, P. aurivella,* *Polyporus versicolor, Daldinia concentrica,* and *Hypoxylon* spp. are aggressive invaders of these larger wounds *(76,104,106)*. *D. concentrica* and *Hypoxylon* spp. also invade branch stubs. Extensive decay is usually associated with larger mechanical injuries more than 20 years old and frost cracks more than 10 years old. Species of *Phialophora* are often found in tissues near frost cracks *(33)*. Bacteria, *Graphium* spp., *Phialophora* spp., *Polyporus* spp., *Pholiota* spp., and *Nectria* are the microorganisms most frequently associated with increment-bore wounds in birch *(60)*. Increment-bore wounds cause reddish-brown decay columns from 74 to 213 cm (29 to 84 in) long within 2 years following boring.

Nectria galligena is the most common and damaging canker disease of yellow birch. It causes perennial target-like cankers, a twig blight, and subsequent crown dieback *(59)*. The fungus can penetrate saplings, small branches, buds, and wounds but usually enters the host through cracks originating at branch axils from heavy snow or ice loads *(7)*. *Nectria* cankers cause localized defects that reduce stem quality and weaken the stem, increasing the chances for wind breakage *(45)*.

Diaporthe alleghaniensis causes a black sunken canker and shoot blight of yellow birch *(1)*. Natural infections probably enter through bud scale scars, frost cracks, leaf scars, wounds, and other injuries *(2)*. Cankers appear on shoots, stems, and petioles of seedlings in the spring and summer and foliage wilts and browns in the summer. Outbreaks of *D. alleghaniensis* occur only when conditions are optimum for infection and growth *(70)*. Normally the fungus is weakly pathogenic and thins out less vigorous and overtopped seedlings.

Gnomonia setacea causes a canker, shoot blight, and leaf spot disease of yellow birch seedlings *(71)*.

Stereum murrayi causes elongated, sunken, bark-covered stem cankers and a yellow-brown stringy trunk rot of yellow birch. Cankers are common on branch stubs and decay usually extends about 0.3 m (1 ft) above and below cankers on pole-sized trees *(106)*. Decay can be extensive in overmature yellow birch. *Phellinus laevigatus* also produces characteristic sunken, bark-covered cankers on mature and overmature trees. Single cankers indicate extensive decay. It is more common on dead than living trees. *Inonotus obliquus* produces black, clinker-like, sterile conks that develop in trunk wounds and branch stubs. Sometimes conks of *I. obliquus* and *Phellinus igniarius* occur on dead branch stubs in the center of Nectria cankers. A sterile conk indicates from 50 to 100 percent cull *(59)* and decay extends from 1.5 to 2.1 m (5 to 7 ft) above and below each conk. *Inonotus obliquus* is an aggressive decay fungi that can invade and kill tissues around these sterile conks *(106)*.

Armillaria mellea, the shoestring root rot, is the most common and important root and butt decayer of yellow birch trees *(106)*. The fungus causes a white root rot with black rhizomorphs on the roots.

Inonotus obliquus, Pholiota spp., *Phellinus igniarius,* and *P. laevigata* are the principal decay fungi of yellow birch trunks *(45,76,106)*. The false tinder fungus *(P. igniarius)* causes a common white trunk rot of yellow birch. A single conk indicates extensive decay that extends 2.4 to 3.0 m (8 to 10 ft) above and below the conk. *Pholiota aurivella* is an aggressive decayer of centers of larger birches and *Pholiota limonella* causes a yellow-brown stringy trunk rot.

Ganoderma applanatum usually occurs on dead birches but sometimes rots the centers of trunks and infects roots and butts through wounds *(106)*. Perennial, hoof-shaped conks of *Fomes fomentarius,* the tinder fungus, are common on dead birch. The fungus also has been associated with decay in living and dead branches of dieback birches. *Piptoporus betulinus, Fomitopsis pinicola,* and *Polyporus lucidus* also are primarily decayers of dead wood but they may extend into centers of living trees *(59)*.

Coniothyrium spp., common twig-inhabiting fungi, injure yellow birch seeds and seedlings *(108)*. They are associated with weevils that tunnel through the cones and destroy or injure the seeds.

The bronze birch borer *(Agrilus anxius)* is the most serious insect pest of yellow birch. It attacks both healthy and weakened birches *(83)* but apparently can normally complete its life cycle only in dead or dying wood in weakened trees. Mature and overmature trees left severely exposed after logging and in lightly stocked stands are more subject to attack then trees in well-stocked stands. Adults deposit their eggs in bark crevices of upper branches. Grubs hatch, bore meandering tunnels underneath the bark that cause top dying, then move progressively lower down the stem and kill the tree within 2 or 3 years. The Columbian timber beetle *(Corthylus columbianus)* bores deep into the sapwood of vigorous birches of all sizes *(3)*. A flatheaded borer *(Chrysobothris sexsignata)* occurs commonly on birch in the East. The ambrosia beetle *(Xyloterinus politus)* is a secondary insect that attacks weakened and wounded birches. Adults bore holes through lenticles in the bark and make galleries *(105)*.

In outbreaks, the birch skeletonizer *(Bucculatrix canadensisella)* completely destroys foliage by August. Successive attacks reduce host vigor and may predispose birches to bronze birch borer attacks.

Although yellow birch is not a preferred host of the forest tent caterpillar *(Malacosoma disstria)*, the gypsy moth *(Lymantria dispar)*, the elm spanworm *(Ennomos subsignarius)*, the hemlock looper *(Lambdina fiscellaria)*, or the saddled prominent *(Heterocampa guttivitta)*, caterpillars of these species defoliate birch in severe outbreaks. Two to three years of successive defoliation can kill birch trees *(122)*. Dusky birch sawfly larvae *(Croesus latitarsus)* prefer small saplings of gray birch but also defoliate yellow birch saplings by feeding inward along leaf edges *(3)*. The lace bug, *Corythucha pallipes*, can be a very injurious insect, especially on young birch *(25)*. A treehopper *(Carynota stupida)*, a stink bug *(Elasmuche lateralis)*, an aphid *(Euceraphis betulae)*, a lygaeid bug *(Kleidocerys resedae germinatus)*, and a scale insect *(Xylococculus betulae)* are other commonly to abundantly occurring sucking insects of yellow birch *(3)*. *E. lateralis* and *Kleidocerys resedae germinatus* also feed on catkins. The birch seed midge *(Oligotrophus betheli)* lives in birch seed and makes it infertile.

Yellow birch is a preferred food of the snowshoe hare and the white-tailed deer. White-tails are especially fond of browsing seedlings during the summer, and green leaves and woody stems in the fall, and they favor succulent sprouts over slower growing seedlings. Heavy or repeated browsing often kills seedlings. Moose often severely browse it. Porcupine feeding often damages birch crowns, reduces wood quality, and sometimes kills the trees. Red squirrels cut new germinants, eat seeds, store mature strobiles, and feed on birch sap.

Yellow birch is a favorite summer food source of the yellow-bellied sapsucker on its nesting grounds. Heavy sapsucker feeding can reduce growth, lower wood quality, or even kill birch. The common redpoll and many other songbirds eat yellow birch seed. Ruffed grouse feed on the catkins, seeds, and buds.

Special Uses

Yellow birch lumber and veneer are used in making furniture, paneling, plywood, cabinets, boxes, woodenware, handles, and interior doors. It is one of the principal hardwoods used in the distillation of wood alcohol, acetate of lime, charcoal, tar, and oils *(9)*.

Genetics

Population Differences

Yellow birch shows great phenotypic variability *(17,28)*. Significant variation in catkin, fruit, and vegetative characteristics have been reported among birch stands throughout its range *(15,30,102)*.

A range-wide study of 55 provenances indicated random variation in seedling height and diameter growth but clinal variation in growth initiation and cessation *(17)*. Similarly, when seedlings grown from seed sources collected along latitudinal and elevational gradients in the Appalachian Mountains were tested, stage of leaf flushing was closely related to latitude but elevation had no influence on stage of flushing and time of growth cessation was more closely related to latitude than elevation *(101)*. Thus, seasonal patterns of shoot elongation and the onset of dormancy in yellow birch appear to be under strong genetic control and probably evolved as an adaption to different photoperiods *(16)*. Temperature, however, is also an important factor affecting the breaking of dormancy and cessation of growth *(17,101)*, and provenances differ in their chilling requirements. Even though the maximum cold hardiness attained in dormant twigs did not vary by geographic seed source *(44)*, overall hardiness apparently does. Seedlings from southern seed sources and low elevations suffered more winter injury in the nursery than those from northern and eastern sources *(24)*.

After 5 years, northern seed sources survived better than southern sources in three northern field plantings, but height growth was not related to geographic origin *(20)*. Results of these studies indicate the importance of collecting seed for planting from superior local phenotypes growing on sites similar to the intended planting site.

Within-population variability in morphology, phenology, and growth of yellow birch is large and often exceeds among-population variation. Within-stand variation has been reported in catkin and fruit characteristics *(15)*, bark color and exfoliation *(28)*, and periodicity of shoot growth *(18,101)*. After 5 years in the field, yellow birch families showed within-stand variation in survival, height, diameter, and crown size *(23)*.

Races and Hybrids

Yellow birch trees with fruiting bracts 8 to 13 mm (0.3 to 0.5 in) long have been called var. *macrolepis* (Fern.) Brayshaw. However, because long-bract specimens more than 8 mm (0.3 in) occur throughout the natural range of yellow birch *(15,29,102)*, it should not be considered a separate variety. Variety *fallax* (Fassett) Brayshaw is distinguished by its dark brown bark that does not exfoliate in thin shreds as much typical yellow birch bark and resembles bark of nonexfoliating *Betula lenta* L. This dark-barked form occurs in southern Michigan, southern Minnesota, and southern and central Wisconsin, northern Indiana, and northeastern Ohio *(17,27)*.

Yellow birch hybridizes naturally with low birch (*Betula pumila* L. var. *glandulifera* Reg.) This hybrid (*B.* × *purpusii* Schneider) can be separated from its parents by differences in leaf blade length, blade width, stomatal length, leaf apical angle, number of teeth per side of leaf blade, and pollen diameter *(29)*. Murray birch (*Betula murrayana*) is a new hybrid from southeastern Michigan. It appears to be an octoploid derivative of an unreduced gamete of Purpus birch and a reduced gamete of yellow birch. Murray birch has larger pollen grains and leaf stomata than its supposed ancestors and larger leaves and fruits than Purpus birch *(4)*. Mountain paper birch (*B. papyrifera* var. *cordifolia* (Regel) Fern.) is the natural cross between yellow birch and paper birch (*B. papyrifera* Marsh.). F_1 hybrids are intermediate between their parents in most characteristics but they can be separated by their bark color and texture, samara body width and pubescence, bract lobe length, amount of bractcilia, and the number of leaves per short shoot *(5)*. This hybrid grows better than yellow birch and withstands greater environmental stress *(22)*. At 27 years of age, *B. lenta* × *B. alleghaniensis* hybrids were about 0.9 m (3 ft) shorter in height and 23 mm (0.9 in) smaller in diameter than intraspecific crosses of their parent species *(100)*.

Through controlled pollination the interspecific hybridity of yellow birch and the following species has been verified: *B. papyrifera* Marsh., *B. pumila* L., *B. lenta* L., *B. glandulosa* Michx., *B. pendula* Roth., *B. davurica* Pall., *B. nigra* L., *B. occidentalis* Hook., *B. populifolia* Marsh., *B. mandshurica* (Reg.) Nakai, and *B. pubescens* J. F. Ehrh. *(17,68,72)*.

B. alleghaniensis is a hexaploid with normal vegetative cells having 42 pairs of chromosomes. Although some counts as high as 49 have been reported, most provenances have chromosome counts of 42 with a range between 37 and 49 pairs *(17)*.

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Betula lenta L. Sweet Birch

Betulaceae Birch family

Neil I. Lamson

Sweet birch (*Betula lenta*), also commonly referred to as black birch or cherry birch, was at one time the only source of oil of wintergreen. It is the aroma of wintergreen emanating from crushed leaves and broken twigs to which this birch owes its common name, sweet. Its specific name, *lenta*, is derived from the tough yet flexible twigs that characterize the species. The wood is also unique. When exposed to air it darkens to a color resembling mahogany and, in times past, was used as an inexpensive substitute for the more valued tropical wood.

Habitat

Native Range

Sweet birch (figs. 1, 2) is primarily a tree of the northeastern United States. It grows from southern Maine westward in southern Quebec, New Hampshire, Vermont, New York, and southeastern Ontario to eastern Ohio; and south in Pennsylvania through the Appalachian Mountains to northern Alabama and Georgia. Forest survey data indicate

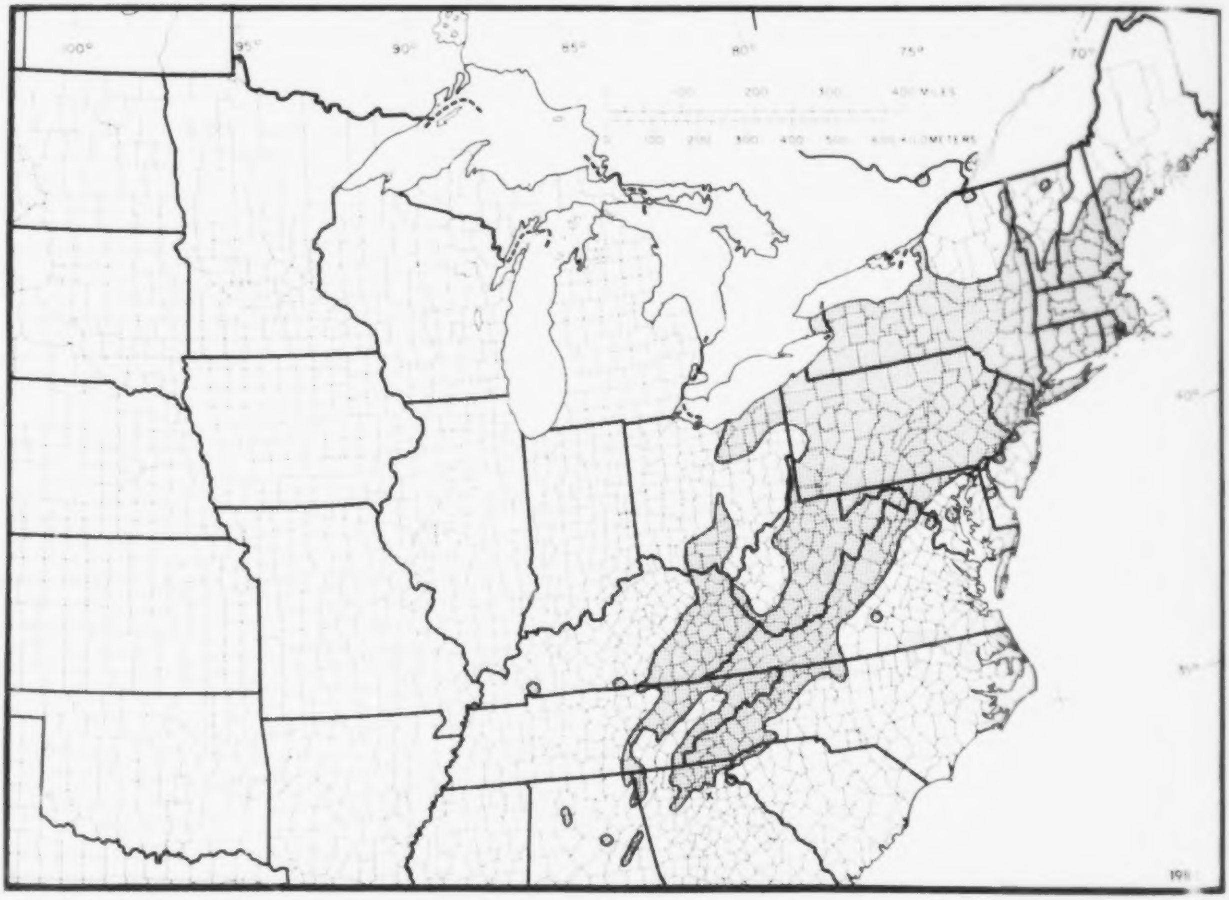

Figure 1—*The native range of sweet birch.*

The author is Forester, Northeastern Area State and Private Forestry, Radnor, PA.

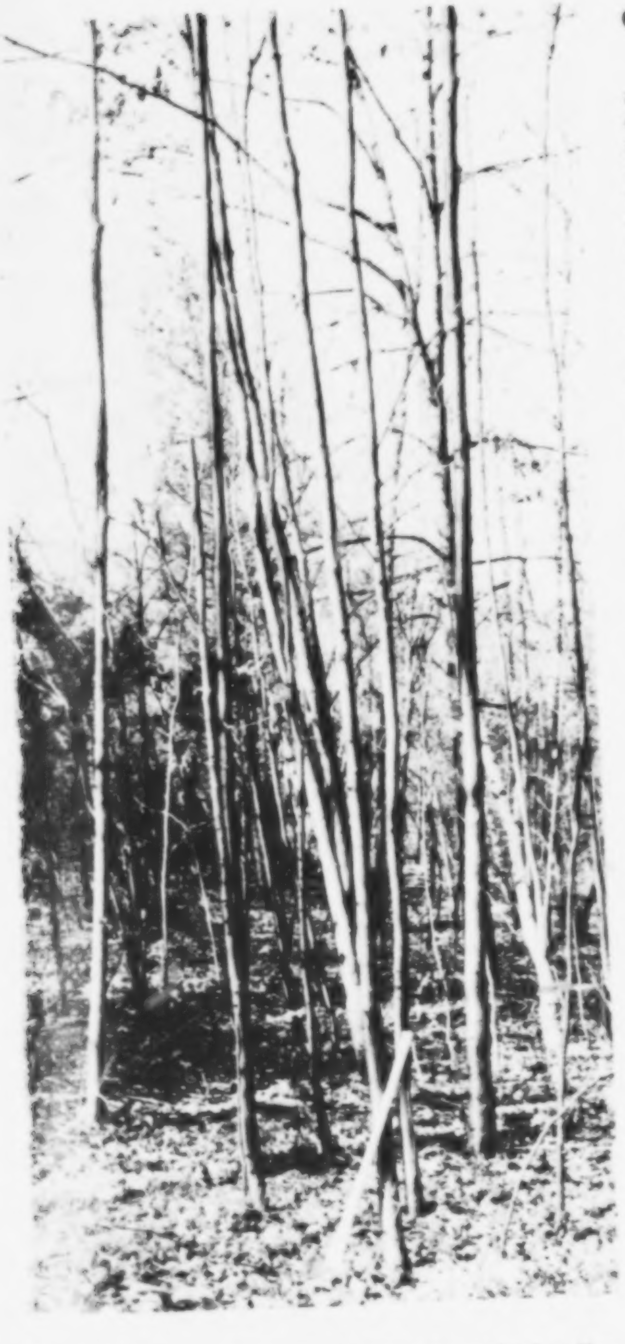

Figure 2—Young 20- to 30-year-old stand of sweet birch in New Jersey.

that sweet birch is most abundant in Massachusetts, Connecticut, New York, and Pennsylvania.

Climate

Precipitation in the range of sweet birch averages about 1140 mm (45 in) a year, about half of it falling during the growing season. In the northern part of the range, snowfall averages 200 to 250 cm (80 to 100 in) a year. Average annual temperature is about 7° C (45° F) in the north and about 13° C (56° F) in the southern Appalachians. The July average is 21° C (70° F) in New England and 23° C (74° F) in the southern Appalachians. Mean January temperatures are -9° to -7° C (15° to 20° F) in New England and -1° to 4° C (30° to 40° F) in the southern Appalachians. The growing season varies from 90 to 220 days, depending on latitude and elevation.

Soils and Topography

Sweet birch grows primarily on three soil orders: Spodosols, Inceptisols, and Ultisols. It grows best on moist, well-drained soils but is also found on a variety of less favorable sites with rocky coarse-textured or shallow soils (7). Because it is occasionally abundant on rocky mountains in Pennsylvania, sweet birch may be valuable for soil protection. On other poor soils, however, such as the excessively dry portions of the Harvard Forest in Massachusetts, sweet birch is partially or completely replaced by oaks and conifers.

Sweet birch grows over a wide range of altitudes from near sea level along the New England coast to an upper extreme of 1220 to 1370 m (4,000 to 4,500 ft) in the southern Appalachian Mountains. In New England, the species is fairly common in southern Maine, the highlands of New Hampshire, western Vermont, the highlands of Massachusetts and Rhode Island, and throughout Connecticut. In the southern Appalachians, where sweet birch grows best, the optimum elevation is between 610 and 1370 m (2,000 and 4,500 ft).

Moist, protected northerly or easterly slopes are considered most favorable for sweet birch in both northern and southern parts of its range.

Associated Forest Cover

Sweet birch is a minor species in 12 Society of American Foresters cover types (*3*):

19	Gray Birch–Red Maple
20	White Pine–Northern Red Oak–Red Maple
21	Eastern White Pine
22	White Pine–Hemlock
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
27	Sugar Maple

28	Black Cherry–Maple
39	Black Ash–American Elm–Red Maple
57	Yellow-Poplar
58	Yellow-Poplar–Eastern Hemlock
59	Yellow-Poplar–White Oak–Northern Red Oak

In the southern Appalachian region, sweet birch reaches its best development in Types 21, 22, 25, 57, 58, and 59.

Important associated tree species include yellow-poplar (*Liriodendron tulipifera*), basswood (*Tilia* spp.), white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), northern red oak (*Quercus rubra*), white birch (*Betula papyrifera*), gray birch (*B. populifolia*), hemlock (*Tsuga* spp.), and eastern white pine (*Pinus strobus*). Understory vegetation varies with locality, but commonly associated shrubs are mountain maple (*Acer spicatum*), striped maple (*A. pensylvanicum*), flowering dogwood (*Cornus florida*), downy serviceberry (*Amelanchier arborea*), American hornbeam (*Carpinus caroliniana*), and eastern hophornbeam (*Ostrya virginiana*). Associated herbaceous vegetation includes Solomons-seal (*Polygonatum pubescens*), marsh blue violet (*Viola cucullata*), clubmosses (*Lycopodium* spp.), mayapple (*Podophyllum peltatum*), trilliums (*Trillium* spp.), jack-in-the-pulpit (*Arisaema atrorubens*), and a variety of ferns. In former clearcut areas where young stands are established, blackberry (*Rubus* spp.) is abundant.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sweet birch flowers are monoecious and borne in catkins. Staminate catkins are formed in late summer or autumn and open in the spring after elongating to about 20 mm (0.75 in). Pistillate catkins appear with the leaves and are borne terminally on short, spurlike branches. Flowers open in April and May. Seeds ripen from about mid-August through mid-September and are contained in erect strobili *(1)*.

Seed Production and Dissemination—Seed fall is during mid-September through November. Seed dispersal is normally by wind and seeds may be blown some distance over crusted snow. Nothing is known about quantities of seeds produced or how far they are spread. Seed production begins when trees are about 40 years old; large seed crops are produced every 1 or 2 years. Cleaned sweet birch seeds average 1,367,000/kg (620,000/lb) *(1)*.

Recommended storage conditions for birch seeds are 1 to 3 percent moisture content at 2° to 3° C (36° to 38° F) *(1)*. Stratification does not generally improve germination, but best germination is obtained when seeds are tested under light *(1)*.

Seedling Development—Under forest conditions, seeds normally germinate during the spring after they are dispersed. Nursery experience indicates that germination may extend over 4 to 6 weeks. Germination is delayed when the embryo is dormant. Moist mineral soils, rotten logs, and humus are suitable germination media.

In nursery practice, birch seed is usually sown in the fall after collection in the late summer or fall. Seeds are broadcast and covered as lightly as possible or not at all if the seedbed is to be kept moist. Epigeal germination is usually complete 4 to 6 weeks after sowing.

Seedlings require light shade for 2 to 3 months during the first summer. Tree percent is low; only 10 to 20 percent will produce 1-0 seedlings. Desirable seedling density is 270 to 485/m² (25 to 45/ft²). Usually 1-0 and 2-0 barerooted seedlings are planted *(1)*.

Sweet birch seedlings develop best during their early years when protected by side shade or light overhead shade. Scattered individuals frequently grow as advance reproduction in openings in mature stands or under younger stands of light to moderate crown density. In the Harvard Forest, sweet birch is sometimes present in the advance hardwood growth under old-field white pine about 50 to 70 years old *(7)*. On fairly cool, moist sites—sheltered ravines, north to east aspects, or moderately heavy soils—heavy cutting or clearcutting of these stands generally results in a higher proportion of sweet birch in the succeeding reproduction than was present in the advance growth. On the other hand, studies in northwestern Pennsylvania have shown that clearcutting of immature second-growth northern hardwood stands before an understory has developed is followed by an abundance of intolerant species with only a poor representation of sweet birch and tolerant hardwoods *(7)*.

Vegetative Reproduction—Sweet birch has been known to reproduce well from small stumps but seems to be less prolific than many of its associates—red maple, sugar maple, beech (*Fagus grandifolia*), yellow-poplar, and northern red oak.

Sapling and Pole Stages to Maturity

Growth and Yield—Sweet birch saplings grow relatively rapidly. The following data have been reported: In northwestern Pennsylvania, at age 12, 1.8 m (6 ft) in height; in western Pennsylvania and central West Virginia, at age 20, 14 m (46 ft) in height and 10 cm (4 in) in d.b.h.

On the very best sites, sweet birch grows 21 to 24 m (70 to 80 ft) tall and 61 to 152 cm (24 to 60 in) in d.b.h. In most areas, however, it is a tree of medium size, 15 to 18 m (50 to 60 ft) tall and 61 cm (24 in) or less in diameter. One of the largest trees on record is 147 cm (58 in) in d.b.h. and 21 m (70 ft) tall.

According to a study in virgin hemlock-hardwood stands in northwestern Pennsylvania, sweet birch saplings in the understory grow about twice as fast as hemlock, beech, sugar maple, and red maple, slightly faster than yellow birch, and at about the same rate as black cherry (*Prunus serotina*) (*7*).

Data from plots on apparently average sites in Delaware County, NY, and Forest and Potter Counties, PA, show that sweet birch can attain a diameter at breast height of about 10 cm (4 in) in 20 years, 18 cm (7 in) in 40 years, and 25 cm (10 in) in 80 years (*7*). In unmanaged sites in the anthracite region of Pennsylvania, sweet birch reached 36 cm (14 in) d.b.h. in 85 years on high sites (Site I) and 30 cm (12 in) in 80 years on average sites (Site II). It is estimated that in managed stands, the same sizes would be reached in 10 to 15 years less time (*7*).

In the Pennsylvania anthracite region, periodic cubic volume production begins to decline when the trees are 36 to 41 cm (14 to 16 in) in d.b.h. (*7*); that is, in about 100 years. Older trees are common and two individuals 192 and 265 years old have been found in Pennsylvania (*7*).

Rooting Habit—No information available.

Reaction to Competition—Sweet birch is classed as intolerant of shade. A long, fairly clean bole is developed in dense stands, while low, thick branches are produced on open-grown trees. Sweet birch may seed in heavily after clearcutting in the Appalachian region, but a majority of the stems succumb to competition by age 20 (*4*). Sweet birch is one of the species that has replaced American chestnut in stands where chestnut was once a major component. Sweet birch has been reported to occupy 15 to 20 percent of the basal area of 40-year-old stands in Connecticut (*12*), all-aged stands in southwestern North Carolina (*8*), and 20-year-old even-aged stands in West Virginia. In a 70-year-old even-aged stand in West Virginia, 20 years of uneven-age management did not significantly change the proportion of sweet birch, which remained at about 18 percent of the basal area of stems 13 cm (5 in) and larger in diameter (*13*).

Damaging Agents—In northwestern Pennsylvania, glaze storms have caused appreciable damage to crowns of sweet birch trees. Available data indicate, however, that this species may be rated as intermediate to fairly resistant to glaze in comparison with other northern hardwoods and common associates (*7*). In addition to the primary effects of ice damage in directly reducing crown volume, glaze storms may contribute to the decline and subsequent death of both yellow and sweet birches by allowing wood decay organisms to enter or, possibly, by causing crown deterioration from sudden excessive exposure.

Sweet birch does not seem to be very susceptible to winter killing. The severe winter of 1942–43 partly or completely killed trees of many species in Maine, but sweet birch appeared to be uninjured (*7*).

A study of the effects of the 1930 drought on oak forests in central Pennsylvania indicated that sweet birch is intermediate in drought resistance. Drought-caused mortality reduced basal area by 36 percent for sweet birch, 11 percent for sugar maple, 50 percent for red maple, and 15 percent for white ash (*7*).

Several fungi attack living sweet birch trees, and stems frequently become highly defective at an early age. In unmanaged sawtimber stands in the anthracite region of Pennsylvania, cull exceeded 20 percent of the total cubic-foot volume of trees 43 cm (17 in) in diameter on Site I and 23 cm (9 in) on Site II (*7*). The most important pathogens are white trunk rot (*Phellinus igniarius*), yellow cap fungus (*Pholiota limonella*), and Nectria canker (*Nectria galligena*) (*5*). Sweet birch is one of the most susceptible species to Nectria canker. Cankers on the bole are more serious than branch cankers because they reduce merchantable volume and increase susceptibility to stem breakage.

Sweet birch is easily damaged by ground fires because it has extremely thin bark. Several fires may kill the tree, but even light scorching at the base of the tree will lower its resistance to the attacks of various diseases or insects such as the ambrosia beetle (*Xyloterinus politus*) (*9*).

Several leaf-feeding insects occasionally infest sweet birch. The most prevalent ones are birch tubemaker (*Acrobasis betulella*), birch skeletonizer (*Bucculatrix canadensisella*), oriental moth (*Cnidocampa flavescens*), gypsy moth (*Lymantria dispar*), and dusky birch sawfly (*Croesus latitarsus*) (*6*).

Special Uses

Sweet birch wood is quite similar to yellow birch (*2*). Lumber and veneer of the two species often are not separated in the market, although production of yellow birch far exceeds that of sweet birch. Sweet birch is used for furniture, cabinets, boxes, woodenware, handles, and millwork, such as interior finish and flush doors. Paper pulp made from sweet birch is used in various amounts with other pulps to produce such products as boxboards, book and newsprint paper, paper toweling, and corrugated paper. Birch oil has been produced commercially from sweet birch bark, but its use has declined with the introduction of synthetic products.

Genetics

Sweet birch is closely related to yellow birch. Efforts to cross the two species have been successful, but the F_1 hybrids have low vigor and seed germination rates *(11)*. No natural hybrids have been verified.

Virginia round-leaf birch, *Betula uber*, at one time was classified as *Betula lenta* var. *uber*. The known population of this species consists of 12 mature trees, 1 sapling, and 21 seedlings in Smythe County, VA *(10)*. In 1978, it was officially listed as an endangered species.

A natural hybrid of *Betula lenta* and *B. pumila* that occurred at the Arnold Arboretum was designated *B. jackii*.

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Betula nigra L. River Birch

Betulaceae Birch family

H. E. Grelen

The most beautiful of American trees—that's what Prince Maximilian thought of river birch (*Betula nigra*) when he toured North America before he became the short-lived Emperor of Mexico (*11*). Also known as red birch, water birch, or black birch (*15*), it is the only birch whose range includes the southeastern coastal plain and is also the only spring-fruiting birch. Although the wood has limited usefulness, the tree's beauty makes it an important ornamental, especially at the northern and western extremes of its natural range (fig. 1).

Habitat

Native Range

The primary range of river birch (fig. 2) is the southeastern quarter of the United States from eastern Texas and southeastern Iowa to Virginia and northern Florida. Scattered populations are found along rivers and streams as far north as southern Minnesota, central Wisconsin, and the middle New England States (*8*). Its northern limit in the Great Lakes region corresponds to the boundary of the terminal moraine of the Wisconsin glacier (*7*). Major exclusions within the primary range are the southern half of the Mississippi River flood plain, the lower coastal plain, the Appalachian Mountains, and limestone areas of southern Missouri, central Tennessee, and central Kentucky. In western North Carolina, river birch is found primarily below 550 m (1,800 ft) elevation but has been found as high as 670 m (2,205 ft) (*17*). Mountainous exclusions may be related to the scarcity of alluvium along streams at higher elevations and faster current streams that sweep seeds downstream (*7*).

Climate

With its geographic range encompassing almost the eastern half of the United States, river birch grows throughout a wide range of climate. It is most abundant in the hot, humid Southeast where the frost-free season averages from 210 to 270 days and annual rainfall averages about 1270 mm (50 in). At the northern extreme of its range in Minnesota and Wisconsin, annual precipitation averages less than 760 mm (30 in) and the frost-free season is 150 days or less (*8*).

Soils and Topography

Although river birch is primarily a plant of alluvial soils (Entisols), it occasionally becomes established on dry soils. The western limit of its range coincides roughly with the eastern boundary of the prairie soils. A study in North Carolina indicated a positive correlation of total clays with presence of river birch stands. The same study found that the tree not only tolerated high soil moisture but also required soils that maintain soil moisture near field capacity yearlong (*17*).

Despite its affinity for water, river birch is only moderately resistant to flooding, a characteristic that may account for its absence on much of the Mississippi River flood plain. Its high tolerance for acid soils is illustrated in Ohio, where it is the primary invader and dominant on stream bottoms made too acid (pH 2 to 4) for other bottom-land trees by coal mine drainage (*10*).

Associated Forest Cover

As river birch is primarily a streambank tree, a list of its associates includes practically all bottomland plants in the eastern half of the United States. Published lists of associated plants from several states provide an east-to-west cross section of the range of river birch. Individual lists are from specific areas, however, and may not be representative of the state as a whole. Associates reported from more than one state are listed below (N = North Carolina, O = Ohio, I = Illinois, M = Missouri):

sycamore	*Platanus occidentalis* (N,O,I,M)
red maple	*Acer rubrum* (N,O,I)
silver maple	*Acer saccharinum* (O,I,M)
black willow	*Salix nigra* (N,O,I)
hazel alder	*Alnus serrulata* (N,O,I)
American hornbeam	*Carpinus caroliniana* (N,O)
honeylocust	*Gleditsia triacanthos* (O,I)
yellow-poplar	*Liriodendron tulipifera* (N,O)
black tupelo	*Nyssa sylvatica* (O,I)
black cherry	*Prunus serotina* (N,O)
American elm	*Ulmus americana* (O,I)

Other associated species include sugar maple (*Acer saccharum*), boxelder (*Acer negundo*), yellow buckeye (*Aesculus octandra*), water hickory (*Carya aquatica*),

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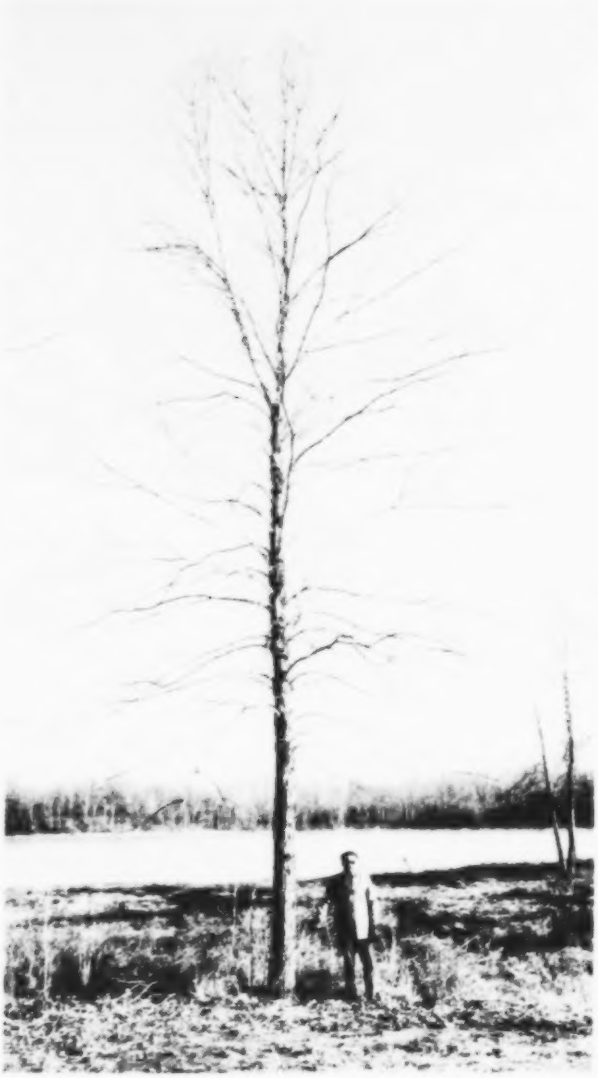

Figure 1—*River birch in winter on a natural site in Illinois.*

bitternut hickory (*C. cordiformis*), mockernut hickory (*C. tomentosa*), hackberry (*Celtis occidentalis*), buttonbush (*Cephalanthus occidentalis*), American beech (*Fagus grandifolia*), swamp-privet (*Forestiera acuminata*), ash (*Fraxinus* spp.), Carolina silverbell (*Halesia carolina*), water-elm (*Planera aquatica*), eastern cottonwood (*Populus deltoides*), swamp cottonwood (*Populus heterophylla*), swamp white oak (*Quercus bicolor*), overcup oak (*Q. lyrata*), bur oak (*Q. macrocarpa*), swamp chestnut oak (*Q. michauxii*), pin oak (*Q. palustris*), northern red oak (*Q. rubra*), baldcypress (*Taxodium distichum*), and American basswood (*Tilia americana*).

A forest cover type, River Birch–Sycamore (Society of American Foresters Type 61), has been described as growing along streams or lake shores with several of the associated species named above. River birch also is listed with associated vegetation in Cottonwood (Type 63) and Sycamore–Sweetgum–American Elm (Type 94) but undoubtedly occurs in most bottom-land types within its range (*4*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—River birch is monoecious; separate male and female flowers are on the same plants. Clusters of pollen-producing male (staminate) catkins are formed at twig tips in fall and mature in April or May of the following year. Pollen production is abundant (birch pollen is a heavy contributor to the hay fever problem) (*13*). Female (pistillate) seed-producing catkins are borne on spur-shoots and appear with the leaves. The flowers open in early spring and the fruit matures in late spring or early summer. It is the only birch that does not produce seed in fall. Good seed crops occur almost every year.

Seed Production and Dissemination—Seeds of river birch are the largest of all the birches native to the United States, averaging 826,700/kg (375,000/lb). Each seed is about 4 mm (0.15 in) long by 3 mm (0.12 in) wide, excluding the wings. The small, winged seeds are transported by wind or by the streams along which river birch grows most abundantly. Seeds germinate rapidly in moist alluvial soil and often form thickets on sandbars.

Seeds can be collected by picking or stripping the "cones" (strobili) while they are still green enough to prevent shattering. Seeds are removed by flailing and screening or fanning.

Seedling Development—Germination of river birch seeds is best (about 35 percent) with unstratified seeds under artificial light (*1*). Germination is epigeal. During early stages, seedlings are fast-growing and have a high soil moisture requirement. Because of abundant seed production, rapid germination, and vigorous early growth, river birch is one of the pioneer species of new forests growing on stream bank alluvium (*17*). Germination and development, as well as growth at all stages, is inhibited by even moderate shade (*3*). Despite the high moisture requirement of seedlings, river birch can tolerate flood-

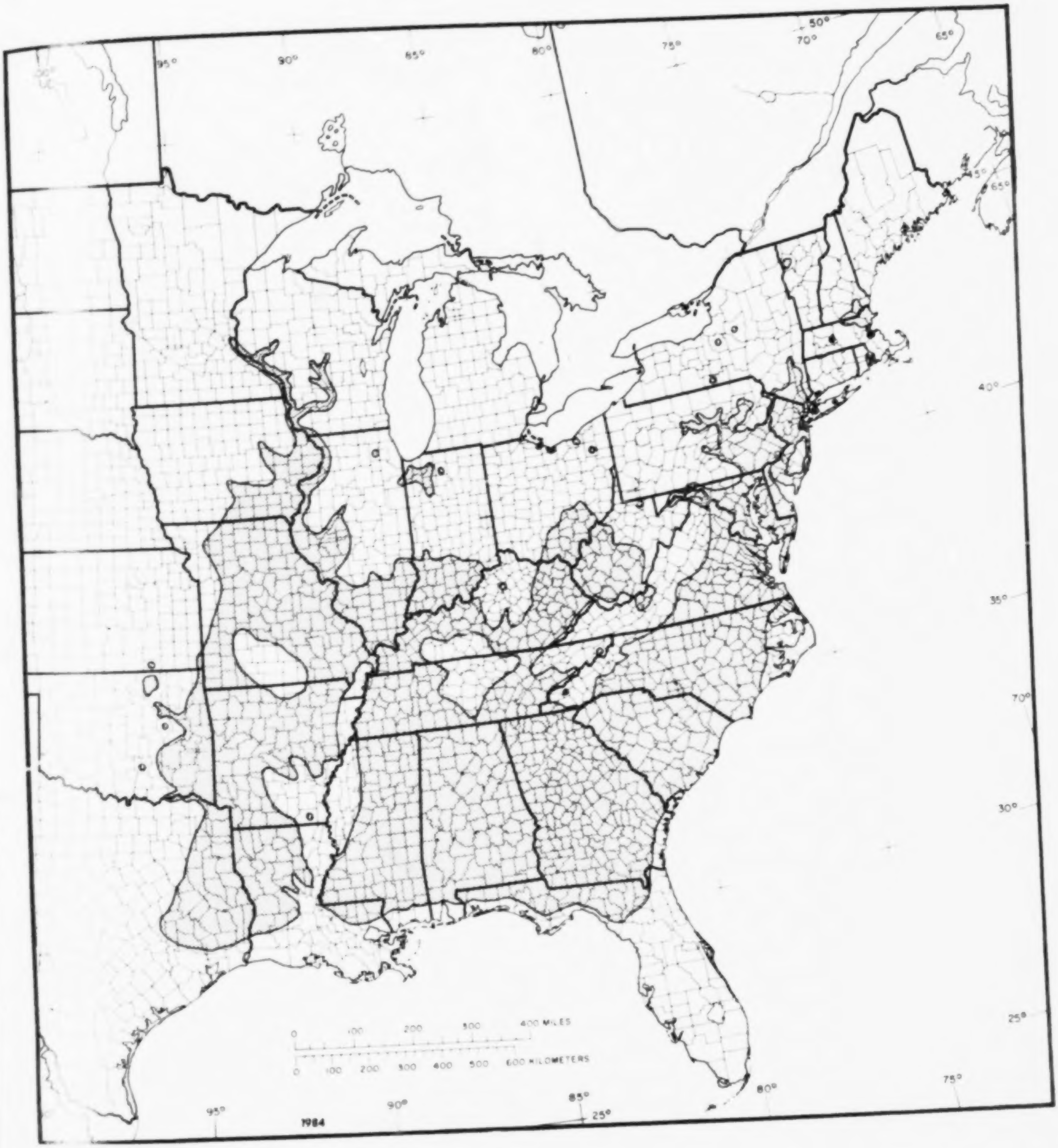

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Figure 2—The native range of river birch.

ing no more than 3 months during the growing season *(14)*. Stumps of young trees sprout vigorously *(5)*.

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—Information on growth and yield of river birch is scarce because most commercial use of the tree comes from natural stands, and wood of river birch is combined with that of other birches, beech, and maples *(3)*. The clear bole is relatively short, with several ascending major branches arising from 4.6 to 6.1 m (15 to 20 ft) above the ground. Multiple stems, probably originating from stump sprouts, are common and tend to have basal sweep. In the lower Mississippi River Valley, isolated trees attain heights of 30.5 m (100 ft) and diameters of 150 cm (60 in). Average merchantable size, however, is 15.2 to 24.4 m (50 to 80 ft) tall and 61 to 91 cm (24 to 36 in) in d.b.h. In Ohio, 58-year-old river birches grown in plantations average 23 to 41 cm (9 to 16 in) in d.b.h. and 15.5 m (51 ft) tall. Trees of the same age grown in the open with no competition from other trees are 58 to 76 cm (23 to 30 in) in d.b.h. and 15.2 to 19.8 m (50 to 65 ft) tall *(11)*.

Rooting Habit—No information available.

Reaction to Competition—River birch is most commonly classed as intolerant of shade. This characteristic precludes uneven-aged management of the species, although no record has been found of commercial planting for wood production. Thick natural stands often stagnate at an early age; nearly 20,000 3-month-old seedlings were counted in a 3.3 m^2 (36 ft^2) plot on a Mississippi River bottom in Wisconsin *(7)*.

Damaging Agents—Floods and floating ice periodically destroy or damage young riverbank stands of river birch, but young trees are usually free of serious disease. Anthracnose leaf blight caused by the fungus *Gloeosporium betularum* is the principal leaf disease. Christmas mistletoe *(Phoradendron serotinum)* is a common pest in the South because of the tree's preference for low, wet sites. It is usually disease-free unless old or damaged *(5)*. Although river birch is host to several species of insects, it has no serious insect pests.

Special Uses

River birch is used mainly for local enterprises such as the manufacture of inexpensive furniture, basket hoops, and turned articles. Experiments in North Carolina did not indicate that it is desirable for commercial pulpwood production, but naturally occurring merchantable-sized trees are often harvested for pulpwood when mixed with other bottomland hardwoods. Strength of the wood makes it suitable for the manufacture of artificial limbs and children's toys. As the wood weighs about 560 kg/m^3 (35 lb/ft^3), it is somewhat lighter than commercially important birches *(3)*. Because of its tolerance to acid soils, river birch has been used successfully in strip mine reclamation. It has also been used in erosion control *(13)*. Its graceful form, attractive bark, and high resistance to the bronze birch borer *(Agrilus anxius)* make it desirable for ornamental planting, especially in the Northeastern and Midwestern States. Young bark varies in color from silvery gray to light reddish brown or cinnamon colored and is lustrous with darker, narrow, longitudinal lenticels. Bark on fast-growing young trees may peel into papery strips. On older trees, bark on branches may be gray, smooth, and shiny; on the main trunk it may vary from dark reddish brown to gray or almost black with inch-thick irregular scales (fig. 3). Seeds are sometimes eaten by birds and the foliage is browsed by white-tailed deer *(15)*.

Genetics

Population Differences

There are few genetic studies of river birch but parent trees from Illinois, Indiana, and Kentucky varied randomly in leaf and seed characteristics. Their progenies also varied in leaf traits, and first-year seedling height was correlated with annual diameter growth of the parent trees *(12)*. Texas stands varied significantly in wood specific gravity, and the variation was correlated with diameter growth. Single-tree progenies also varied significantly in height growth *(6)*. Thus, it appears possible to increase both growth and specific gravity of river birch by selecting for fast diameter growth.

Hybrids

Natural hybrids between river birch and paper birch *(Betula papyrifera)* have been reported but have never been verified and appear unlikely because interspecific hybridization involving river birch is very difficult. River birch has been crossed with

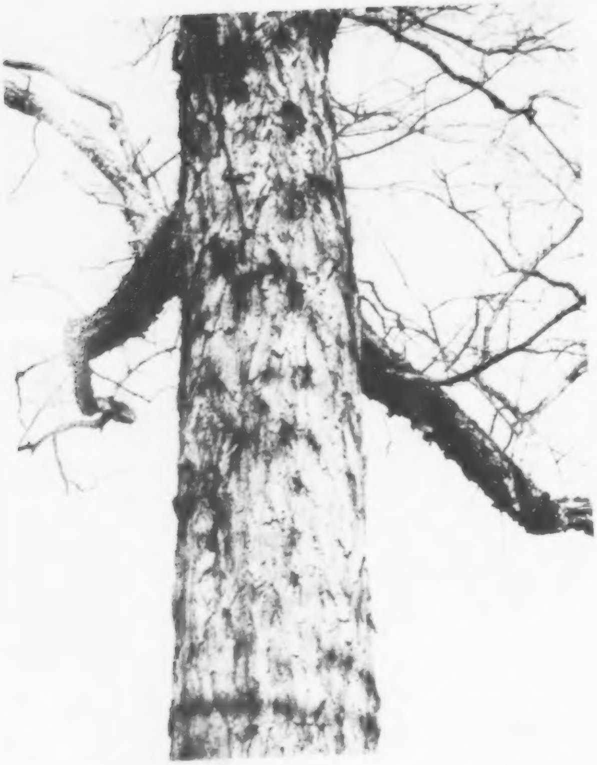

Figure 3—*Bark of a large river birch at the Secrest Arboretum in northern Ohio.*

sweet birch (*B. lenta*), gray birch (*B. populifolia*), paper birch (*B. papyrifera*), resin birch (*B. glandulosa*), and low birch (*B. pumila* var. *glandulifera*) and with the following introduced species: *B. ermani* Cham., *B. raddeana* Trautv., *B. pendula* Roth, *B. pubescens* Ehrh., *B. platyphylla* Sukachev, and *B. maximowicziana* Regel. Seed yield and viability have been low and growth has been poor. In general, crossing attempts are more likely to succeed if river birch is the female parent (*2*).

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Betula papyrifera Marsh. Paper Birch

Betulaceae Birch family

L. O. Safford, John C. Bjorkbom, and John C. Zasada

Typical paper birch *(Betula papyrifera* var. *papyrifera)*, also called white birch, canoe birch, or silver birch, and the other five intergrading geographical varieties, western paper birch *(B. papyrifera* var. *commutata* (Regel) Fern.), mountain paper birch *(B. papyrifera* var. *cordifolia* (Regel) Fern.), Kenai birch *(B. papyrifera* var. *kenaica* (W. H. Evans) Henry), Alaska paper birch *(B. papyrifera* var. *neoalaskana* (Sarg.) Raup), and northwestern paper birch *(B. papyrifera* var. *subcordata* (Rydb.) Sarg.) are the most widely distributed birches in North America, mostly in Canada. These medium-sized, fast-growing trees develop best on well-drained, sandy loams on cool moist sites. They are commonly found in the mixed hardwood–conifer forests but may form nearly pure stands where they pioneer areas disturbed by fires or logging. Paper birch is short-lived and rarely lives more than 140 years. Commercially the lumber is used for veneer, pulpwood, and many specialty items. The handsome foliage and showy white bark make the trees attractive for landscaping. They are important browse plants for animals, and the seeds, buds, and bark are also eaten by wildlife.

Habitat

Native Range

The range of paper birch (figs. 1, 2) closely follows the northern limit of tree growth from Newfoundland and Labrador west across the continent into northwest Alaska; southeast from Kodiak Island in Alaska to British Columbia and Washington; east in the mountains of northeast Oregon, northern Idaho, and western Montana with scattered outliers in the northern Great Plains of Canada, Montana, North Dakota, the Black Hills of South Dakota, Wyoming, Nebraska, and the Front Range of Colorado; east in Minnesota and Iowa, through the Great Lakes region into New England. Paper birch also extends down the Appalachian Mountains from central New York to western North Carolina *(46,58,97,112)*.

Climate

Paper birch is a northern species adapted to cold climates. Its range is bounded on the north by the 13° C (55° F) July isotherm and in the south, it seldom grows naturally where average July temperatures exceed 21° C (70° F). In Alaska, paper birch is found on the cooler north and east aspects and aspen on the warm south and west aspects. The variety *cordifolia* in the east generally grows in the cooler habitats—upper elevations on mountains near tree line in the southern part of the range and on cooler north aspects and in depressions toward the northern part of its range.

Paper birch tolerates wide variations in the patterns and amounts of precipitation. In Alaska, annual precipitation averages only about 300 mm (12 in); more than half of this as rain in summer and fall. At higher elevations in eastern mountains, precipitation averages as high as 1520 mm (60 in). In general, the climate where paper birch is found has short cool summers and long cold winters during which the ground is covered with snow for long periods *(39,46,67,97)*.

Soils and Topography

As might be expected from its wide range and genetic diversity, paper birch grows on almost any soil and topographic situation ranging from steep rocky outcrops of the mountains to flat muskegs of the boreal forest (Histosols). Best development and growth are on the deeper well-drained to moderately well-drained Spodosols, Inceptisols, and Entisols common to glacial deposits throughout its range. In Alaska, best development occurs on Inceptisols developed on loess deposits. Paper birch was found in all habitats described for the White Mountains of New Hampshire and occurred in 50 percent or more of the plots in six of these habitats. Poorest site-index values were obtained for the driest and wettest sites of the range sampled, whereas higher values were obtained for the moist and nutrient enriched habitats *(56)*.

In New England, paper birch tends to be more abundant on the dry sites than on the wet or poorly drained soils *(46,63)*. In Alaska, where paper birch and aspen *(Populus tremuloides)* occur in mixed stands, birch predominates on the cooler, moister sites, and aspen on the warmer, drier sites. Birch

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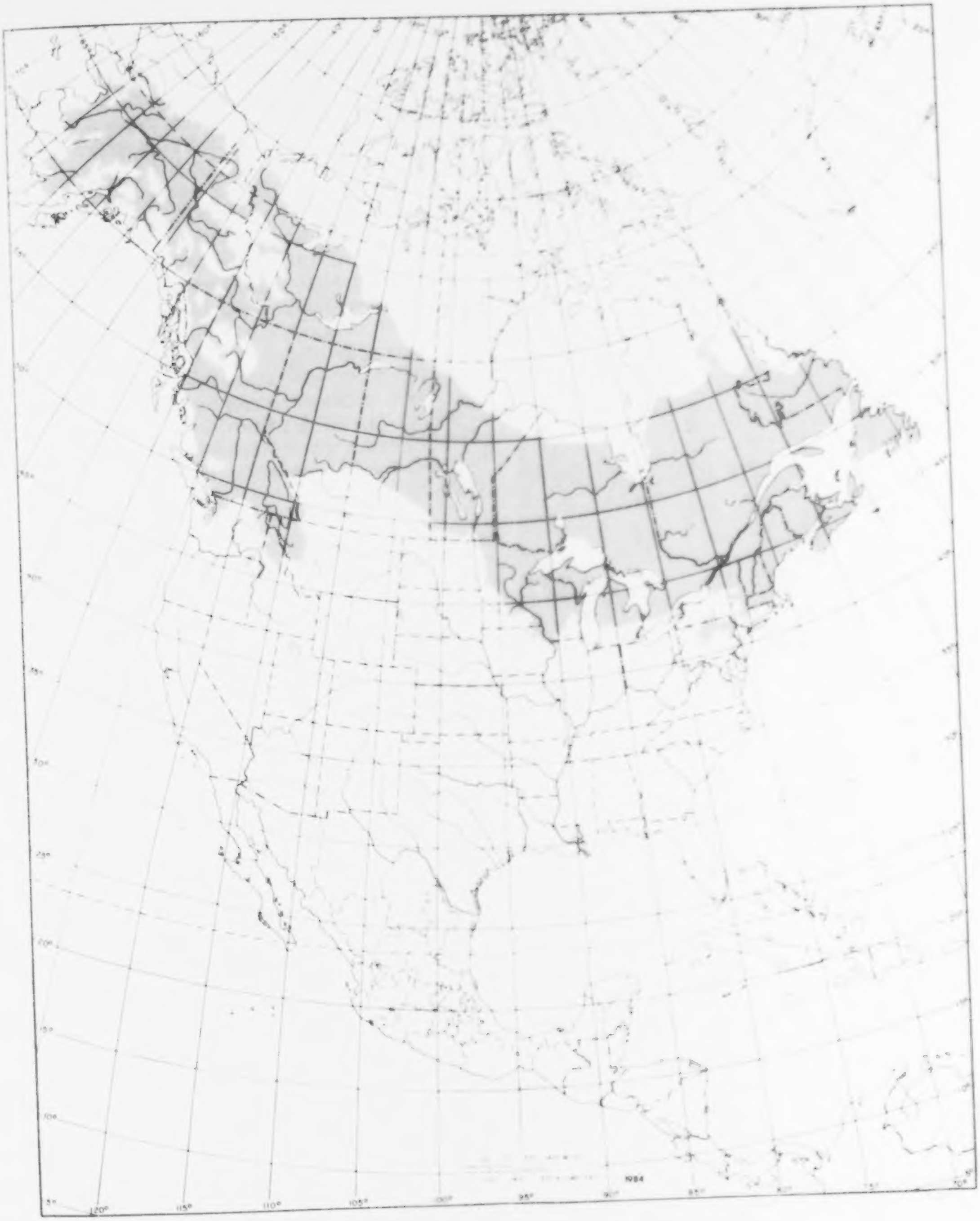
The authors are all Research Foresters: Safford and Bjorkbom (deceased), Northeastern Forest Experiment Station, Radnor, PA, and Zasada, Pacific Northwest Research Station, Portland, OR.


120°
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100°
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1984

Figure 1—*The native range of paper birch.*

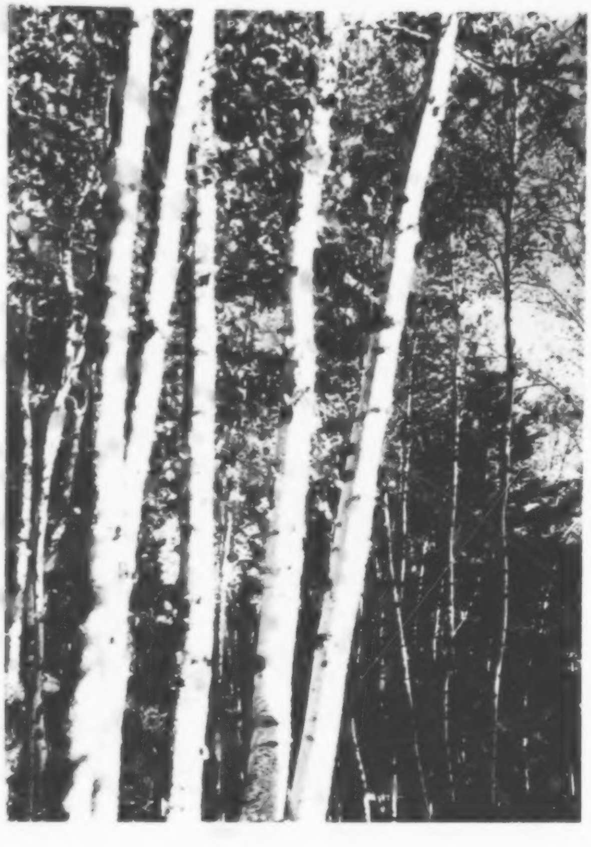

Figure 2—*Paper birch.*

also can be found with black spruce *(Picea mariana)* on north-facing slopes *(67)*.

Typical soil temperatures of birch stands in the Fairbanks region of Alaska range from 9° to 11° C (48° to 52° F) at a 10 cm (4 in) depth during the June to August growing season *(112)*. Paper birch grows best in soils free of shallow permafrost. But on north slopes, vigorous sapling birches have been observed where the annual depth of thaw in permafrost was only 64 to 76 cm (25 to 30 in) *(67)*.

Paper birch litter contributes to the nutrient status of the forest floor. When compared with red pine *(Pinus resinosa)*, litter under birch was found to be enriched with calcium, potassium, magnesium, phosphorus, and boron and reduced in manganese, aluminum, iron, and zinc. Enrichment extended into the top 3 cm (1.2 in) of the mineral soil where concentrations of calcium, nitrogen, phosphorus, magnesium, potassium, and volatile matter and pH were increased. These increases resulted from the more rapid rate of decomposition of litter under birch than under red pine *(93)*. In Alaska, biomass averaged 60 to 70 t/ha (27 to 31 tons/acre) with an annual litter fall of 4 to 8 t/ha (1.8 to 3.6 tons/acre). In birch stands, rain in the form of throughfall contained from one-half to one-third the calcium and magnesium and twice as much manganese as throughfall under aspen *(112)*. Acidity of precipitation decreased as it passed through crowns of paper birch and other species in New Brunswick, Canada. However, acidity of stemflow increased for paper birch, red pine, white pine, red spruce, and black spruce, where as acidity of stemflow decreased for aspen, red maple, and white spruce *(60)*. Total forest floor biomass and content of magnesium, iron, and manganese were greater and calcium was less under birch than aspen *(95)*.

Soils under birch and aspen tend to be warmer but drier than soils under the softwoods. Consequently, CO^2 production is limited by lack of moisture under these two hardwoods and by low temperature under the conifers *(82)*.

Paper birch tolerates fairly high levels (up to 80 mg/l) of aluminum in nutrient solution with no reduction of root growth (64). This tolerance varies significantly among provenances with some tolerating much higher levels (up to 120 mg/l) *(90)*. Radicle elongation of paper birch seed germinated on filter paper treated with 1 to 5 mg/l of copper, nickel, or cobalt was reduced about 25 percent. Higher concentrations of these elements (up to 100 mg/l) were required for reduction of radicle elongation on mineral or organic soil. Conifer seeds were less sensitive than paper birch to the same treatments *(71)*.

Associated Forest Cover

Paper birch is a common associate of 38 northern forest types. In the east and central regions, it is a major component of two forest cover types *(29)*: Paper Birch (Society of American Foresters Type 18) and Paper Birch–Red Spruce–Balsam Fir (Type 35). In Alaska and western North America, it is an integral member in three types: Paper Birch (Type 252), White Spruce–Paper Birch (Type 202), and Black Spruce–Paper Birch (Type 254).

Paper birch forms either pure stands or mixtures of varying proportions in all regions. Pure stands are generally succeeded by other species *(57)*, but some remnant birch can be maintained in openings in stands of other species thought to be climax for a given locality *(47)*. In other instances, intimate mixtures with long-lasting types are characteristic. In the Laurentian highlands of eastern Canada, aspen and birch stands establish within 30 years following fire. Pure stands of conifers—jack pine or black spruce—follow. As the conifers age and openings occur, paper birch re-enters the stands, becoming a younger component of the mature conifer forests. Fire returns at about 130-year intervals *(20)*.

Shrubs commonly associated with paper birch in the eastern part of its range are beaked hazel *(Corylus cornuta)*, common bearberry *(Arctostaphylos uva-ursi)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, wintergreen *(Gaultheria procumbens)*, wild sarsaparilla *(Aralia nudicaulis)*, blueberries *(Vaccinium* spp.), raspberries and blackberries *(Rubus* spp.), American and redberry elder *(Sambucus canadensis* and *S. callicarpa)*, and hobblebush *(Viburnum alnifolium)*.

Shrubs common to the Alaskan interior paper birch type are American green alder *(Alnus crispa)*, Scouler willow *(Salix scouleriana)*, highbush cranberry *(Viburnum edule)*, Labrador-tea *(Ledum groenlandicum)*, raspberry *(Rubus* spp.), and roses *(Rosa* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Paper birch flowers from mid-April through early June depending on location. The flowers are monoecious *(8)*. In the late summer, staminate flowers are preformed in aments (catkins) 2 to 2.5 cm (0.75 to 1 in) long at the ends of twigs and lateral shoots. These mature and grow in length to 4 to 10 cm (1.5 to 4 in) in the following spring. Pistillate flowers are borne in cylindrical aments (catkins) 2.5 to 5 cm (1 to 2 in) long and 8 mm (0.33 in) in diameter on the same tree. Two or three (rarely four) aments cluster on lateral spur shoots and disintegrate when mature. Fruits are winged nutlets 1.5 mm (0.06 in) long by 0.8 mm (0.03 in) wide with styles 0.8 mm (0.03 in) long. The shape of bracts of the pistillate catkins is characteristic for the species, and variations are useful in distinguishing varieties. The seeds ripen from early August until mid-September. Seed dispersal begins soon after ripening and occurs earlier in injured trees than in healthy trees *(46)*. Some seeds fall as early as July as a result of birds feeding on the developing catkins.

Seed Production and Dissemination—Under normal conditions, paper birch begins producing seeds at about 15 years of age, and optimum seed-bearing age is 40 to 70 years. However, seedlings grown in pots for one extended growing season in a greenhouse produced viable seeds (66 percent germination capacity) during the second season of growth under natural conditions out-of-doors *(79)*. In mature stands, good seed crops occur every other year on the average, but some seeds are produced in most areas every year. Seed years vary with locality, so information specific to the area of interest is required for planning regeneration treatments. Some information can be gained by observing male catkins the fall before a seed year. An abundance of male catkins may mean a potentially good seed year, because both biotic and abiotic factors can destroy a potentially good crop. Lack of male catkins means a poor seed year. In average seed years, nearly 2.5 million seeds per hectare (1 million/acre) are produced and bumper years have 86 million or more seeds per hectare (35 million/acre). In a mature stand in Alaska, total dry weight of catkins was 6.8 kg (15 lb) per tree, yielding almost 9 million seeds *(106)*. Discolored and empty seeds make up 14 to 47 percent of the crop, the lowest proportion of empty and discolored seeds occurs in the best seed years *(4,7,8,63,108)*.

Some paper birch seeds may be collected from August through the following spring, but most are dispersed during the months of September through November in both the eastern and western portions of the range *(4,107)*. In Alaska, some seeds were caught in seed traps every month. The rate was less than 10 million/ha (4 million/acre) for December through August whereas it averaged 70 to 90 million/ha (28 to 36 million/acre) for September through November *(106)*. Time of dispersal does not depend on size of seed crop *(7)* but varies among stands and from year to year depending upon weather conditions. Seeds that fall in late fall and winter have higher germination capacity than those that fall early *(4)*.

Extremely heavy seed crops can result in crown deterioration and reduced growth. In an Ontario stand, foliage was dwarfed or missing; buds in terminal portions of branches did not develop; and terminal growth and diameter growth were reduced when an extremely heavy seed crop was produced *(41)*.

The light, winged paper birch seeds (3 million/kg or 1.4 million/lb) are dispersed readily by the wind, and some seeds travel great distances, particularly when blown across the surface of snow. However, the majority of seeds fall within the stand where they are produced, and seedfall drops off rapidly with distance from the stand edge into clearcut openings. When seedfall within an undisturbed stand was compared with seed fall in a clearcut, seed catch was reduced by 40 percent at the stand edge and 90 percent at the center of the 100-m (330-ft) square opening. On the basis of these observations, it was estimated that a seed crop of 5 million/ha (2 million/acre) would be required to regenerate openings as large as 50 m (165 ft) wide *(4)*. Similar results were obtained in Alaska where 30 to 40 million seeds per hectare (12 to 16 million/acre) were estimated at 40 m (132 ft) from the stand edge, and 0.5 to 0.7 million/ha (0.2 to 0.3 million/acre) were estimated at 100 m (330 ft) *(106)*. Seed crops in interior Alaska are adequate for regeneration of clearcuts as wide as 30 m (100 ft) at least 1 in every 4 years *(108)*.

Under test conditions, paper birch seeds need no pretreatment for germination if tested under light at 20° to 25° C (68° to 77° F) *(8,26,104)*. Seeds germinate in the dark if given either a prechilling or red light treatment; the red light effect can be reversed by far-red light, indicating that germination readiness is phytochrome mediated *(2)*. Germination at low temperatures 5° to 10° C (41° to 50° F) under light is also enhanced by prechilling *(26)*.

In the field, germination generally follows one of two patterns: either germination starts as soon as environmental conditions are suitable and continues until all viable seed have germinated *(19)*; or an initial burst of germination is followed by a period of low germination as seedbeds dry out, and when rainfall replenishes soil moisture, a second peak of germination occurs later in the summer *(110)*.

The proportion of sound, viable seed varies greatly among seed lots of paper birch. This proportion of viable seed can vary among seed years, localities, and specific mother trees *(2)*. Some individuals may produce heavy seed crops frequently with consistently low (10 percent or less) germination *(106)*. The percentage of viable seed can be estimated by examining embryo development with transmitted light under a dissecting microscope *(8)*.

Paper birch seed may be stored for at least 2 years at room temperature if the moisture content is maintained at less than 5 percent *(8)*. Longer storage, up to 8 years, with only slight loss of germination capacity is possible when seeds are stored at 2° to 4° C (35° to 40° F) in sealed containers and at low moisture *(17,79)*. After long storage, viability of each seed lot should be verified by a germination test before the seeds are used, because some seed lots do lose viability *(17)*.

Seedling Development—Germination is epigeal *(8)*. Because of the small size of paper birch seed, newly germinated seedlings are very fragile. They are sensitive to moisture, temperature, light, and seedbed condition *(46)*. Best germination occurs on mineral soil; germination on humus is reduced by about 50 percent, and germination on undisturbed litter is only 10 percent of that obtained on mineral soil. Shaded sites produce about twice as many germinants as full-sun sites. In a partially wind-thrown conifer forest, paper birch seedlings colonized windthrow pit and mound microsites, but most established seedlings were on rotting logs, stumps, and tree boles *(100)*. Early survival of seedlings follows similar patterns, but initial height growth is better on humus than on undisturbed sites, probably because of greater nutrient availability. At the end of the first growing season, birch seedlings growing in full sunlight on mineral soil averaged 5 cm (2.0 in) tall compared with 12 cm (4.7 in) for those on humus. Maximum heights on the same seedbeds were 42 cm (16.5 in) for seedlings on humus and 20 cm (7.9 in) for those on mineral soil. Heights of seedlings in shaded locations on those same seedbeds were about one-half the maximum values *(61,62)*. However, paper birch may grow well in about 50 percent of full sunlight. In a study of response to shading, paper birch seedlings grew taller under 45 percent sunlight than when grown in 100, 25, or 13 percent of sunlight. Total dry weight was equal for seedlings grown under 45 percent and 100 percent full sunlight *(59)*.

In Alaska, 3 years following clearcutting, scarified sites were 100 percent stocked, with an average of 1.7 million birch seedlings per hectare (0.7 million/acre). Unscarified seedbeds were only 30 percent stocked with an average of 50,000 seedlings per hectare (20,000/acre) *(109)*. Paper birch seedlings averaged 28 cm (11 in) in height on the scarified plots and 5 cm (2 in) on the unscarified plots after 2 years *(112)*. This difference in results from those in the Northeast is probably caused by severe competition from herbaceous and other vegetation that became established on the unscarified plots. On an upland black spruce site subjected to burning treatments, best germination, survival, and 3-year growth occurred on heavily burned microsites *(111)*.

After 5 years, in a Maine site-preparation study, there were more paper birch seedlings on disked sites than on burned or logged-only sites. But, after 10 years, the total number of birch seedlings, as well as the number of potential crop trees, was greater on the burned treatment than on either the disked or logged-only treatments *(3,5)*:

Treatment	Thousands of seedlings		Potential crop tree	
				Height
	5 yr	*10 yr*	*10 yr*	*10 yr*
			per ha	*m*
Burn	47	12	1191	2.1
Disk	124	8	232	1.5
Log only	25	4	497	2.1
			per acre	*ft*
Burn	19	5	482	7
Disk	50	3	94	5
Log only	10	2	201	7

Following clearcutting or other disturbances, the bulk of paper birch regeneration becomes established during the first growing season from seeds that fell the previous fall and winter. Data for Alaska indicate that 88 percent of seedlings present at age 5 germinated during the first growing season following clearcutting and scarification, 8 percent during year 2, and 4 percent during year 3. About 20 percent of the first-year germinants were still alive after 5 years: 7.4 million/ha (3 million/acre) the first year and 1.7 million/ha (0.7 million/acre) the fifth year *(110)*. Some birch seed may lie dormant in the forest floor for a year or more, especially following heavy seed crops and dry years when conditions for germination are poor *(31,34,38,112)*. This dormant seed may be an important source of germinants in poor seed years *(74)*.

Seedlings of the variety *cordifolia* are slower growing than typical paper birch. When planted together under similar conditions in Quebec, typical paper birch grew to a height of 3.0 m (9.8 ft) in 5 years against 1.2 m (3.9 ft) for variety *cordifolia* *(13,39)*.

In the Northeast, clearcutting stands younger than 100 years to regenerate paper birch often results in severe competition from large numbers of seedlings of *Rubus* spp. and pin cherry (*Prunus pensylvanica*), so that weeding or cleaning is needed to ensure satisfactory birch stocking *(61)*. Large numbers of seeds of these species are stored in the forest floor in stands younger than 100 to 120 years old *(36)*. Longer rotations are recommended to diminish the population of stored seeds and the consequent competition following disturbance.

Even though natural regeneration of paper birch is obtained readily, planting of seedlings may sometimes be desired *(45)*. In planting old fields, site preparation to remove sod is required for satisfactory survival and growth. Protection from girdling by rodents and browsing by deer may be required in some locations *(6)*. Planting stock can be either conventional bare-root stock or container-grown seedlings *(35)*.

Seasonal height growth often begins while minimum temperatures are below freezing, rises gradually to a peak of maximum growth in mid-June, and then drops off gradually. Compared to other species, paper birch has a long period of height growth. Seedling height growth may be prolonged indefinitely under long-day conditions, whereas short days cause terminal growth to stop *(27,46)*.

Diameter growth starts after maximum temperatures reach 21° C (70° F) or more and minimum temperatures are above freezing. Temporary abrupt increases and decreases in diameter growth in the spring and fall are correlated with a sudden rise and fall of temperature but not with rainfall. Diameter growth ceases well before either moisture or temperature becomes limiting. In general, paper birch begins and ceases diameter growth later than most of its associates *(46)*.

Vegetative Reproduction—Paper birch can regenerate from sprouts following cutting or fire. Prolific sprouting usually occurs when young, vigorous trees have been cut in the spring to stump heights of 15 to 30 cm (6 to 12 in) *(46)*. Whereas sprouts are seldom abundant enough to reproduce mature stands, they can be valuable supplements to seedlings, particularly on droughty or other difficult sites *(63)*. In an early study of mature stands in Maine, 77 percent of the stumps sprouted, but only 27 percent had live sprouts after 2 years. Heavy browsing by deer was an important factor in sprout mortality *(46)*. In Alaska, 85 to 99 percent of the paper birch stumps sprouted in stands as old as 55 years of age. Sprouting decreased to less than 50 percent in stands greater than 125 years old *(106)*. Ten years after clearcutting and site preparation in a 70-year-old stand in Maine, sprouts were 34 percent of the potential crop trees on logged-only sites. Severe site preparation treatments of disking and burning reduced the number of sprouts as potential crop trees from 299/ha (121/acre) in the winter-logged treatment to 67/ha (27/acre) on burned plots and 32/ha (13/acre) on disked plots *(5)*. Sprouting also may occur at the base of standing live trees that have been subjected to increased exposure by removal of nearby trees *(46)*. Sprouts tend to mature earlier (age 50 to 60 years) and deteriorate sooner (age 70 to 90 years) than trees of seedling origin. Final quality is usually lower for sprouts *(63)*.

Paper birch can be propagated by grafting, air-layering *(18)*, rooting of cuttings, or tissue-culture techniques. Cuttings from seedlings root sooner and at higher percentages than cuttings from mature trees. Eighty percent of stem and branch cuttings from 8- to 10-week-old paper birch seedlings rooted within 45 days when placed in 10 percent Hoagland's solution (no. 2) under a 16-hour photoperiod *(44)*. Apical cuttings collected in July from 18-year-old paper birch and treated with indolebutyric acid (IBA) rooted better than cuttings collected on earlier or later dates with or without IBA treatment. Some individual trees consistently rooted better (over 40 percent), others consistently poorer (less than 20 percent), regardless of date of collection or hormone treatment of the cuttings *(73)*. Stem segments and axillary buds from new germinants or 1- to 2-year-old seedlings proliferate into callus and multiple plantlets on a medium containing zeatin and adenine sulphate. These plantlets can be successfully

Table 1—Yield of fully stocked stands of paper birch in Alaska *(40)*, Ontario *(72)*, and New England *(63)* by site index

Site index and location	Stand age in years 30	40	50	60	70	80
			m³/ha			
13.7 m						
Alaska	—	—	16	46	76	103
Ontario	11	40	65	84	96	101
New England	51	88	122	148	167	185
16.8 m						
Alaska	—	23	62	107	147	177
Ontario	35	72	105	133	152	165
New England	63	108	150	180	205	226
19.8 m						
Alaska	10	54	118	180	231	267
Ontario	59	104	145	180	209	230
New England	74	128	177	213	242	267
			ft³/acre			
45 ft						
Alaska	—	—	*229*	*657*	*1,086*	*1,471*
Ontario	*157*	*571*	*929*	*1,200*	*1,371*	*1,443*
New England	*729*	*1,257*	*1,743*	*2,114*	*2,386*	*2,643*
55 ft						
Alaska	—	*329*	*886*	*1,529*	*2,100*	*2,529*
Ontario	*500*	*1,029*	*1,500*	*1,900*	*2,171*	*2,357*
New England	*900*	*1,542*	*2,143*	*2,571*	*2,929*	*3,229*
65 ft						
Alaska	*143*	*771*	*1,686*	*2,571*	*3,300*	*3,814*
Ontario	*843*	*1,486*	*2,071*	*2,571*	*2,986*	*3,286*
New England	*1,057*	*1,829*	*2,529*	*3,043*	*3,457*	*3,814*

transplanted to pots in a greenhouse and subsequently into the field *(65)*. High rooting percentages in mature birch can be restored by establishing young plants through tissue culture techniques for a source of cuttings *(92)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Young paper birch (fig. 3) grows rapidly. Individual trees often have a diameter of 20 cm (8 in) after 30 years. With age, the growth rate declines, and in old age it becomes almost negligible *(46)*. Trees in mature stands average 25 to 30 cm (10 to 12 in) in d.b.h. and 21 m (70 ft) in height. On the best sites, an occasional tree in old stands may exceed 76 cm (30 in) in d.b.h. and 30 m (100 ft) in height. Trees of the variety *cordifolia* are as large as 102 cm (40 in) in d.b.h. *(46,99)*.

Yields at maturity on good sites are similar for Alaska, Ontario, or New England at 230 to 270 m³/ha (3,286 to 3,857 ft³/acre) (table 1). On poor sites, yields range from about 100 to 185 m³/ha (1,429 to 2,643 ft³/acre). New England stands produce the greatest yields for all age classes and site qualities. Yields in Ontario are greater than those in Alaska for the first few decades, but growth rate of Ontario stands near maturity declines more rapidly than that of Alaskan stands. Thus, by age 80, Alaskan yields surpass those from Ontario on all sites (table 1) *(40,63,72)*. The range of site index is similar for New England, New York, and the Lake States, 12 to 24 m (40 to 80 ft) at base age 50 years *(22,23)*; and somewhat lower for Alaska, 11 to 20 m (35 to 65 ft) *(40)*, indicating a lower growth potential, probably because permafrost and cold soils limit the growth of birch on many sites.

Paper birch is considered a short-lived species. Trees mature in 60 to 70 years, and few live longer than 140 to 200 years *(46)*. The variety *cordifolia* apparently has a longer life span. Several trees on Mt. Washington in New Hampshire were more than 200 years old; the oldest was 225 *(37)*. Stands appear to last longer in Alaska than in more southerly regions *(40)*.

Mortality is heavy throughout the life of a paper birch stand. Individual trees express dominance early in life. Unless suppressed trees are released early, they soon die. Intermediate trees survive longer but gradually succumb after struggling for years at a low rate of growth *(46)*. Initial stem diameter at the seedling and small sapling stage can be used to predict relative growth potential of trees selected for release. Trees that averaged only 0.8 cm (0.3 in) in diameter when released grew to 5.3 cm (2.1 in) in diameter after 24 years; trees in the same stand that were larger than 2.0 cm (0.8 in) in d.b.h. when released grew to 13.7 cm (5.4 in) in the same time *(53)*.

Rooting Habit—Paper birch is generally a shallow-rooted species. The bulk of the roots are found in the top 60 cm (24 in) of soil; taproots do not form. Rooting depth depends on soil depth and varies among forest stands and from tree to tree within stands *(75)*. High wind will break the bole of paper birch more often than it will uproot the tree. Broken stems generally sprout *(100)*. Rootlets with a primary xylem diameter greater than 25 percent of total diameter tend to become part of the permanent woody root system. Rootlets with a smaller diameter primary xylem are ephemeral *(43,102)*.

Reaction to Competition—Paper birch is classed as a shade-intolerant tree. Among its common associates in the Northeast, only aspen, pin cherry, and gray birch *(Betula populifolia)* are more intolerant. In the natural succession of species, paper birch usually lasts only one generation and then is replaced by more tolerant species *(46)*. When growing in mixture with spruce or spruce-fir, birch often retains a position in the stand, and the stands do not go toward pure spruce climax *(22,67,76)*. Birch persists in some Alaskan spruce stands because of a physical smothering of spruce seedlings by birch foliage, or in other instances, chemical properties of the ashes of birch following fires may inhibit spruce development *(67)*.

In declining old-growth stands of white spruce *(Picea glauca)* growing on flood plains in Alaska, paper birch invades openings created by death and uprooting of the spruce. Mineral soil exposed by the uprooting, and the rotting wood of the fallen trees, provide suitable seedbeds *(28,52,106)*.

In a study of drought response, paper birch saplings had lower leaf conductance values and higher water potential than white oak *(Quercus alba)* growing under the same soil moisture conditions. The birch trees reached water stress conditions sooner than the oak. The birch trees responded to stress by losing leaves, whereas the white oak was not severely stressed by conditions of the study *(30)*.

In a greenhouse study, paper birch seedlings were less tolerant of flooding than river birch *(B. nigra)*. Once flooding treatments ended, paper birch seedlings grew faster and were as large as unflooded controls at the end of the experiment. Flooded river birch seedlings formed adventitious roots; paper birch did not *(68)*.

Because of its intolerance, paper birch often requires release from faster growing species such as aspen or pin cherry that overtop it in the early stages of regeneration *(53)*. Response depends on degree of release. Generally, the greater the release, the greater the growth response of paper birch. Thinnings in sapling and pole stands also yield increased diameter growth of paper birch crop trees in proportion to the degree of release *(79)*. Stands approaching maturity—more than 60 years—seldom respond to thinning *(33,46)*.

Paper birch is a nutrient-sensitive species. Seedling, sapling, pole, and sawtimber-size trees have all responded to fertilizer treatments in recent studies *(1,24,78,80,94,96)*. In a mixed stand, paper birch responded more than quaking aspen but less than bigtooth aspen *(Populus grandidentata)* to additions of nitrogen, phosphorus, and lime *(24,81)*. Response indicated increased stem wood and bark, branches, and foliage *(84,85)*.

Damaging Agents—In the eastern part of its range, large percentages of paper birch were killed or damaged by a condition called birch dieback during the late 1930's and 1940's. Symptoms include dying back of twigs and branches in the crown, loss of vigor, and eventual death over a period of 5 to 6 years. Trees most often damaged were shallow rooted and showed root mortality before crown symptoms. The root mortality was attributed to environmental conditions *(75)*. Many trees sprouted epicormic branches in the lower crown and bole and eventually recovered. The dieback condition has subsided and currently is not considered an important threat to paper birch *(46,63)*.

Postlogging decadence—a condition resembling birch dieback—sometimes develops in residual trees following partial cutting. The older the stand and the heavier the cutting, the more likely this condition. For example, trees left as seed trees in regeneration cuttings are almost certain to decline and die within a few years. The best way to avoid these problems in managed stands of birch is to maintain vitality of trees through periodic thinnings begun at an early age. Also, heavy partial cuttings in mature previously untreated stands should be avoided *(63)*.

The bronze birch borer *(Agrilus anxius)* is the most serious insect pest of the paper birch. Usually it attacks overmature trees or trees in weakened condition. The borer played a secondary role in the

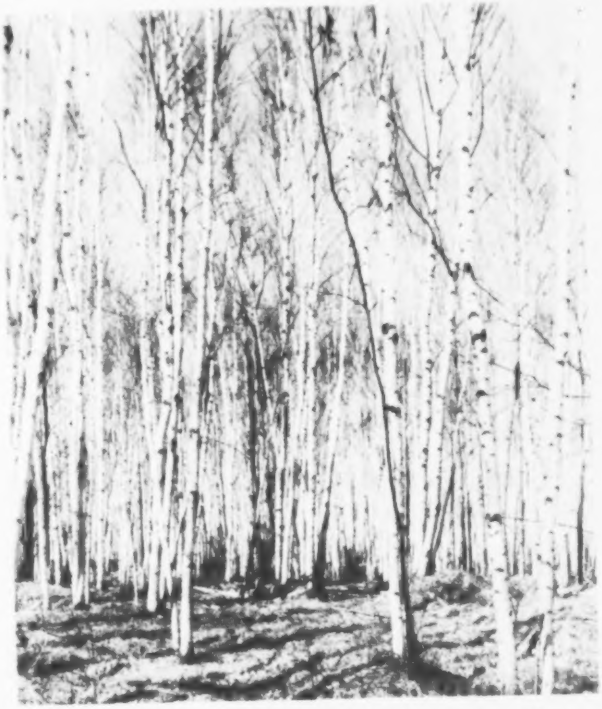

Figure 3—*A 35-year-old stand of paper birch on a very good site in northern Wisconsin.*

dieback outbreak and undoubtedly caused the death of some trees that otherwise might have recovered. To prevent buildup of this insect, weakened and mature trees should be removed from the stand, and injury to residual trees should be avoided *(21)*.

The most serious defoliators of birch are the forest tent caterpillar *(Malacosoma disstria)*, the birch skeletonizer *(Bucculatrix canadensisella)*, the birch leafminer *(Fenusa pusilla)*, birch leaf-mining sawflies *(Heterarthrus nemoratus* and *Profenusa thomsoni)*, the birch casebearer *(Coleophora serratella)*, as well as the general forest defoliators—the saddled prominent *(Heterocampa guttivitta)*, and the gypsy moth *(Lymantria dispar)*, and in Alaska, the spear-marked black moth *(Rheumaptera hastata) (101)*. Defoliation alone seldom causes mortality of otherwise healthy trees. Rather, growth rate is reduced and trees become susceptible to other damaging agents, particularly the bronze birch borer, which attacks and causes death of substantial numbers of trees *(21)*. Cambium miners, such as *Phytobia pruinosa*, and ambrosia beetles, such as *Trypodendron betulae* or *Xyloterinus politus*, make injuries that cause defects in paper birch timber but seldom cause the death of trees *(63,88)*. The variety *cordifolia* may be less susceptible to severe insect attacks than the typical paper birches *(39)*.

Micro-organisms that enter the bole of the tree through wounds or branch stubs cause discoloration and decay in paper birch wood. A condition known as red heart is a very common defect in some areas. The wood is darkened in color but may be sound enough for some uses. Principal decay-causing fungi include *Inonotus obliqua*, *Phellinus igniarius*, and *Pholiota* spp. *(63)*. Stem cankers that ruin the tree for timber purposes and make it unsightly are often caused by *Inonotus obliqua* and *I. glomeratus (87)* and *Nectria galligena*. The root-rotting fungus *Armillaria mellea* infects birch trees, causing cracks at the base of the stem ("collar crack"). Attack by root-rotting fungi can also result in uprooting by the wind *(88)*.

Animals that damage paper birch stands include white-tailed deer, porcupines, moose, and hares. The most serious threat from deer and moose is overbrowsing at the seedling stage, which reduces the amount of dominant birch in regenerating stands or impairs the quality of survivors *(46,51)*. Porcupines damage larger trees by feeding on the inner bark and girdling large branches in the crown and upper trunk. The yellow-bellied sapsucker pecks rows of holes through the bark; these are the source of entry for discoloration and decay organisms and may cause ring shake *(88)*. If a dense band of holes girdles the stem, all or a major portion of the crown will die, leading to a weakened state that can invite attack by the bronze birch borer or decay organisms. In a Maine study, 51 percent of the paper birch trees damaged by sapsuckers died. Damage by hares and other small mammals is of critical importance to the development of planted seedlings *(6)*. Hares clip or gnaw bark on small birch seedlings causing reduction in birch stocking *(51)*. Red squirrels may girdle stems by stripping off the bark *(46)* or wound the tree by biting it to obtain sap *(88)*.

Fire, which is responsible for the establishment of many paper birch stands, is also one of the most serious enemies of established stands. Because the bark of paper birch is thin and highly flammable, even large trees may be killed by moderate fires *(6)*. However, in Alaska, pure birch stands have little fuel available, so fires are not common. Hot crown fires in spruce become slow-burning ground fires when they enter birch stands; the fire may even go out. In extreme drying of deep organic horizons in some birch stands, a hot, slow-moving fire will consume all of the organic matter, leaving the shallow-rooted birch without support. The otherwise undamaged trees soon fall over *(106)*. Paper birch is very susceptible to logging damage during partial harvest treatments using mechanical techniques. Up to 53 percent of designated crop trees sustained injuries to root systems, boles, or both during a careful thinning *(69)*.

Near Sudbury, Ontario, air pollution with heavy metals from mining and smelting operations has created a coppice woodland dominated by paper birch and red maple. Seedlings are repeatedly killed back and sprout from the base, creating multi-stemmed stools. On an exposed ridge, 18-year-old paper birch sprouts averaged 3.3 m (10.8 ft) in height and 5.8 cm (2.3 in) d.b.h. On a more protected site, 21-year-old paper birch sprouts averaged 5.9 m (19.4 ft) in height and 7.8 cm (3.7 in) d.b.h. *(48)*. In the greenhouse study previously mentioned, fumigation with SO_2 caused partial stomatal closure, visible foliar injury, and reduced growth rate of both river and paper birch. Stomatal conductance and SO_2 uptake of flooded seedlings were lower than controls, but SO_2 effects were the same whether flooded or not *(68)*.

People vandalize trees along roadsides and in parks and picnic areas by peeling off strips of the outer papery bark. The trees are seldom killed but always carry unsightly scars. In areas of great scenic value, the exposed inner bark can be painted white to disguise the wound.

Special Uses

Young regenerating stands of paper birch and associated species provide prime browse and cover for deer and moose *(86,91)*. Although pin cherry is preferred over birch as a browse species, birch is more important because it is more abundant *(70)*. In Alaska birch stands produce less browse than aspen but more than willow and alder. Willows are a preferred browse species by Alaskan moose, but birch is preferred to aspen, balsam poplar, or alder. It takes 3 to 5 years following logging, a fire, or other disturbance for production of young trees to begin providing sufficient buds and twigs for browsing animals. Peak browse production occurs from 10 to 16 years after the disturbance. Mature stands have essentially no available browse *(103)*. The browse index for yellow and paper birch in the four northeastern National Forests indicates that birch is preferred 2.5 to almost 5 times more than its abundance would suggest *(86)*.

Paper birch is also an important source of food for birds. The redpoll, pine siskin, and chickadee feed on seeds; the ruffed grouse eats male catkins and buds *(86)*.

The graceful form and attractive white bark of paper birch make it a prized species for ornamental planting and landscaping around homes and public buildings. The main drawback is that bark on young paper birch remains golden or brown in color until about age 10 to 12. For that reason, European birches and some other introduced species that have white bark at earlier ages are more frequently chosen as ornamentals.

Its status as a pioneer species and its adaptability to disturbed sites indicates that paper birch is a prime hardwood species for use in revegetating spoils and other drastically disturbed sites. Paper birch has been planted successfully on acid coal mine spoils. Survival of 2-0 planting stock ranged from 58 to 98 percent on spoils with a pH ranging from 3.0 to 4.0 *(25)*.

Paper birch can be tapped in the spring to obtain sap from which syrup, wine, beer, or medicinal tonics can be made. The carbohydrate content of about 0.9 percent consists of glucose, fructose, and sucrose. This contrasts with the 2 to 3 percent sugar found in the sap of sugar maple. Currently only a few small-scale sugaring operations are in Alaska *(32)*. Sap flow season for birch begins and ends later than for maples. Birch syrup contains lower sugar concentrations than maple (302 and 711 g/l) and is more acidic (pH 5.2 and 6.6) *(50)*.

Paper birch has moderately dense wood. Full tree chips can be used in pulp and paper manufacture, other reconstituted uses, and fuel. Branches contain fewer fibers and more vessels than bole-wood. Branch fibers and vessels are 30 to 50 percent shorter and smaller in diameter than those from boles. Pulp from branch-wood is weaker in mechanical strength than pulp from bole-wood but is suitable for paper making *(54,55)*. Equations for estimating biomass of full trees and various components from tree diameter, height, or both, are available *(49,83,89,105)*. As a fuel, caloric values for paper birch did not differ significantly between samples with and without bark, or between bole and branch components when data for samples with and without bark were pooled *(66)*. Paper birch bark has a high fuel value. Of 24 species tested, it had the highest caloric value per unit weight—5740 cal/g (10,331 Btu/lb)—and the third highest per unit volume—3209 cal/cm^3 (360,569 Btu/ft^3) *(42)*.

Genetics

Population Differences

Paper birch consists of a large, very plastic gene pool. There are six recognized varieties: typical paper birch (var. *papyrifera*), western paper birch (var. *commutata*), mountain paper birch (var. *cordifolia*), Kenai birch (var. *kenaica*), Alaska paper birch (var. *neoalaskana*), and northwestern paper birch (var. *subcordata*) *(58)*. On the basis of morphological characteristics, seedling growth habits, and chromosome numbers, some authors have suggested that var. *cordifolia* be reinstated to specific rank as *B. cordifolia* *(13)*. Chromosome number varies considerably within the species. The somatic chromosome number for typical paper birch can be either 70 or 84, rarely 56. The chromosome number for var. *cordifolia* is consistently 28, and other varieties may be 42, 56, 70, or 84. Seedlings from the same mother tree typically have two or more chromosome counts (9 through 14, 39). In a comparison of morphological and cytological characteristics of the varieties *commutata* and *subcordata*, only bark color was consistently different between the two, suggesting that separate variety names were not justified *(11)*.

Within typical paper birch, selections of superior trees have been made on the basis of growth rate, stem form, and other characteristics. In a greenhouse study, seedlings with a plus-tree mother grew significantly taller and larger in basal diameter than trees with "average" mothers. Also, sources from New Hampshire were superior to sources from Michigan, Vermont, Maine, or Eastern Canada, in that order *(77)*.

Hybrids

Hybridization in the birches is common. Paper birch hybridizes naturally with almost every other native species in the genus *(1,16,58,98)*. The hybrid crosses with yellow (*B. alleghaniensis*), sweet (*B. lenta*), and river (*B. nigra*) birch have not been named. Blue birch (*B.* × *caerulea* or × *caerulea-grandis*) is thought to be a hybrid between grey birch and var. *cordifolia* (*12,39*). The variety *cordifolia* is thought to be a hybrid of paper and yellow birch (*58*). The named hybrids are crosses between paper birch and shrub or small tree species, as follows: Yukon birch (*B.* × *eastwoodiae* Sarg. or *B.*× *commixta* Sarg.) with resin birch (*B. glandulosa*); horne birch (*B.* × *hornei* Butler or *B.* × *beeniana* A. Nels.) with dwarf arctic birch (*B. nana*); Sandberg birch (*B.* × *sandbergii* Britton or *B.* × *uliginosa* Dugle) with bog birch (*B. pumila* var. *glandulifera*); and Andrews birch (*B.* × *andrewsii* A. Nels. or *B.* × *piperi* Britton or *B.* × *utahensis* Britton) with water birch (*B. occidentalis*).

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Calophyllum calaba L. María, Santa-María

Guttiferae Mangosteen family

P. L. Weaver

Maria *(Calophyllum calaba)* is a medium-sized tropical evergreen tree known also as santa-maria or false-mamey. It is frequently used for reforestation. Although it is easily established by direct seeding and grows well in almost all soils, its growth is generally slow. It tolerates salt spray and forms a dense crown with small fragrant flowers that make it popular as a shade tree or a protective hedge. The wood is used widely in the tropics where a strong, moderately durable timber and general utility wood is needed.

Habitat

Native Range

Maria is native to Puerto Rico and the Virgin Islands and widely distributed through the West Indies. It ranges from Mexico through the Guianas to Peru, Bolivia, and Brazil. It is naturalized in Bermuda and has been introduced in southern Florida *(15)*.

In Puerto Rico, it is native to the moist coastal and limestone regions, probably ranging through 150 m (492 ft) in elevation. Elsewhere in the Caribbean, maria is found near the coast at low elevations on moist through wet sites, and occasionally in areas that are inundated during part of the year *(16,18,30,31)*. In northern South America, it is found along river banks and in stream valleys *(25)*. The tree, when established, is capable of growing on degraded soils.

Climate

In Puerto Rico, maría is found naturally in the Subtropical Moist Forest life zone. Annual rainfall varies from about 1500 to 2000 mm (59 to 79 in), with annual evapotranspiration ranging from 1500 to 1780 mm (59 to 70 in). Mean annual temperature is 25° C (77° F) with little variation during the year *(7)*. Plantations, however, have been established in wetter and drier sites including the Subtropical Dry Forest life zone with annual rainfall of only 1000 mm (39 in). Plantation sites in the Cordillera Central and the Luquillo Mountains have annual rainfall as high as 3050 mm (120 in). In Nicaragua, maría occurs in Lowland Rain Forest and Lower Montane Rain Forest *(5)* with annual rainfall ranging from 1980 to 5000 mm (78 to 197 in) *(31)*. In British Honduras *(19)* and elsewhere in the Caribbean, annual rainfall varies from about 1500 to 2500 mm (59 to 98 in). None of these areas has temperatures below freezing.

Soils and Topography

María is native to the sandy soils on the north coast of Puerto Rico where it grows mainly on soils of the orders Inceptisols, Oxisols, and Alfisols. It is also found on coastal sands in the central Lesser Antilles *(4)*. In Puerto Rico, it has been planted in the interior mountains on deep clays and serpentine soils, and on shallow limestone soils at lower elevations near the coast *(22)*. In general, it tolerates degraded sites and a variety of drainage conditions. It may be found on ridges, slopes, coves, flats, and swamps.

In Puerto Rico, maría is not planted on good sites because faster growing species are preferred. It is recommended, however, where erosion has depleted soil fertility, for straight slopes, ridges, and convex slopes *(22)*. In British Guiana and Surinam it grows in freshwater swamps; and in Jamaica it is found on volcanic and metamorphic shales *(2,25)*.

Associated Forest Cover

In Puerto Rico, maría is associated with ucar *(Bucida buceras)*, roble blanco *(Tabebuia heterophylla)*, algarrobo *(Hymenaea courbaril)*, palo de pollo *(Pterocarpus officinalis)*, and palma real *(Roystonea borinquena)*, all in the Subtropical Moist Forest.

Elsewhere within its range, maría is a constituent of several different forest types (table 1) and is found in association with numerous species. In particular, the tree is found in moist to wet primary forest at low elevations, and in secondary forest. In Central America, it is often found in association with caoba hondureña *(Swietenia macrophylla)* and cedro hembra *(Cedrela odorata)* *(18)*. In British Honduras, it is found in successional forests along with the genera *Orbignya*, *Dialium*, *Virola*, *Terminalia*, *Symphonia*, and *Vochysia* *(30)*. In the Lesser Antilles it is associated with almácigo *(Bursera simaruba)*, malagueta *(Pimenta racemosa)*, laurel avispillo *(Nectandra coriacea)*, and cupey *(Clusia rosea)* *(4)*.

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Table 1—Presence of maría (*Calophyllum calaba*) in tropical forests of the Western Hemisphere

Location[1]	Forest type classification[1]	Annual rainfall	
		mm	*in*
Puerto Rico *(15)*	Subtropical Moist Forest, limestone	1500 to 2000	59 to 79
British Honduras *(19)*	Tropical Moist Forest	2000 to 4000	79 to 157
Nicaragua *(31)*	Lowland Evergreen Forest	2000 to 4000	79 to 157
	Lower Montane Forest	3000 to 5000	118 to 197
Jamaica *(1,2)*	Evergreen Seasonal Forest, limestone	2000	79
	Lower Montane Rain Forest	3000	118
Cuba *(25,29)*	Lowland Rain Forest	1500	59
St. Kitts *(4)*	Dry Evergreen Forest	1500	59
Dominica *(4)*	Secondary Rain Forest	2000	79
Martinique *(4)*	Evergreen Seasonal Forest	1500 to 3000	59 to 118
Surinam *(16)*	Marsh Forest	NA[2]	NA
Costa Rica *(13,27)*	Tropical Moist Forest	1000 to 2000	39 to 79
	Tropical Wet Forest	2000 to 4000	79 to 157
	Premontane Wet Forest	2000 to 4000	79 to 157
Venezuela *(10)*	Tropical Moist Forest	1000 to 2000	39 to 79
	Premontane Wet Forest	2000 to 4000	79 to 157

[1] Holdridge *(12,13)*—Puerto Rico, British Honduras, Costa Rica, and Venezuela; Beard *(2,5)*—Nicaragua, Jamaica, Cuba, St. Kitts, Dominica, and Martinique; Lindeman *(16)*—Surinam.
[2] Not available.

Life History

The mature maria tree is easily identified by a combination of characteristics including its opposite, elliptical, dark-green leaves with numerous parallel, lateral veins and very dense foliage (fig. 1). A yellowish sap exudes from broken leaves, twigs, and incisions in the trunk. The bark has many diamond-shaped fissures.

In Puerto Rico, the tree commonly attains a height of 12 to 20 m (39 to 67 ft) and about 45 cm (18 in) in diameter. Where conditions are favorable elsewhere in its range, it sometimes attains a height of 30 to 45 m (100 to 150 ft) and is supported by a straight, unbuttressed bole 90 to 215 cm (35 to 85 in) in diameter. At maturity, maria is a canopy tree with a dense, rounded crown.

Reproduction and Early Growth

Flowering and Fruiting—Maria is polygamous; male and bisexual flowers are borne in 5-cm (2-in) racemes on the same tree. The bisexual flowers have four white, rounded, and concave sepals about 0.65 cm (0.25 in) long; the smaller white sepals are commonly absent. Male flowers have about 40 to 50 stamens in a prominent orange cluster more than 6 mm (0.25 in) across, and often a rudimentary pistil. In Puerto Rico, flowering is chiefly in the spring and summer, and the fruit matures in the fall *(15)*. In Trinidad the normal flowering period is in September and October, but trees flower at other times. The fruits, which are globose, one-seeded drupes, about 2.5 cm (1 in) in diameter, usually ripen the following May or June. Some trees have been observed to flower and fruit when only 3 years old. Good seed years were found to be irregular in Trinidad *(23)* although the tree fruits abundantly on an annual basis in Puerto Rico.

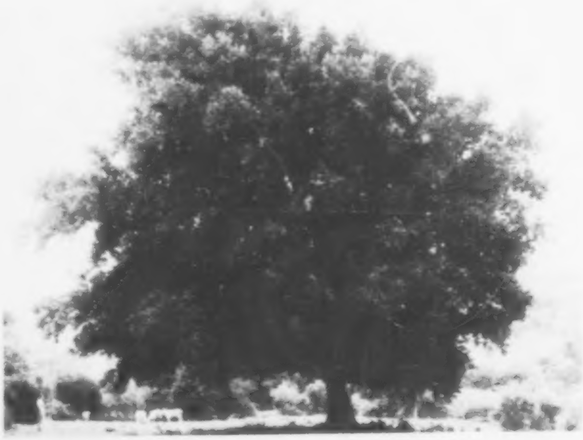

Figure 1—*Open-grown maria showing very dense foliage and spreading crown.*

Seed Production and Dissemination—A substantial portion of the seeds fall below the parent tree where they germinate and form dense stands of seedlings. On steep slopes, however, some are removed by heavy rains.

Seeds maintain their viability well, and a fair germination rate is attained even with seeds that have been stored for 1 year in a dry room. Average germination in Puerto Rico is about 70 percent.

Use of fresh seeds is desirable in the establishment of plantations. Usually seeds are sown directly into the soil and demonstrate a favorable germination capacity except when the seeds are empty.

In Trinidad, the agouti (a tropical rodent) sometimes carries off the fruits and stores them in caches; bats also aid in dispersal *(23)*. In Puerto Rico, birds, bats, and rats are dispersal agents *(21)*.

Seedling Development—During the storage of fruits, the water content should not be lower than 35 percent nor the storage temperature below 0° C (32° F) *(37)*. Germination is hypogeous and occurs within 6 weeks, provided the seeds are sown without an endocarp. Untreated fruits give the same results after 16 weeks. Retarded germination is caused by the endocarp, which inhibits water uptake. The endocarp may be broken by striking with a hammer.

Broadcasting of seeds in suitable conditions results in germination. Plantations, however, are usually established by planting seeds in the ground at a depth of 2.5 cm (1 in) using a dibble. Direct sowing of maría fruits has been done under the light shade of pino australiano *(Casuarina equisetifolia)*, in areas where farmers wanted to perpetuate windbreaks. The seedlings demonstrated nearly 100 percent survival with a height growth of 1.2 m (4 ft) in only 2 years. María has also been seeded within rows of beans that provide shade and protect the seedlings from desiccation *(23)*. In the mountains of northeastern Puerto Rico, where annual rainfall is more than 2500 mm (98 in), fruits were placed in raised piles of earth where they germinated and grew successfully *(11)*.

The first leaves are produced when the seedling is about 10 cm (4 in) tall. When the seedling reaches about 15 cm (6 in), as determined by the reserve food supply in the seed, it often ceases to grow in height while the root system establishes itself. Seeds sown in nursery beds produce plants with a maximum height of 1 m (3 ft) in 1 year.

Several experiments have been conducted with maría seedlings by personnel of the Institute of Tropical Forestry. Seeds pregerminated in wet moss and later planted with radicles or hypocotyls 8 cm (3 in) or under were less successful than dibbled fruits without pretreatment. Bareroot plantings cut to about 10 cm (4 in) in height, in exposed conditions, failed nearly 100 percent because of desiccation. The results were the same in heavy shade. In exposed conditions, transplanting of maría has only been successful when the plants were moved with a ball of earth. Best results are achieved when the transplants are moved during the rainy season.

Vegetative Reproduction—María does not coppice, except when very young, nor does it produce root suckers. Similarly, neither root nor shoot cuttings have been proved successful as a means of establishment.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth of maría at all stages in the life cycle appears to be slow in Puerto Rico. The tree does not reach its maximum size on the island, and most of the growth records are for poor sites.

Plantations in Trinidad and Puerto Rico vary from 22 to 34 years old and show that volume mean annual increment (MAI) ranges from 4.3 to 12.6 m^3/ha (61 to 180 ft^3/acre) (table 2). Height MAI varies from 0.6 to 1.4 m (2.0 to 4.6 ft) and diameter MAI from 5.6 to 13.8 mm (0.22 to 0.54 in). Crude estimates of biomass MAI range between 2.2 and 6.4 metric t/ha (0.98 and 2.86 tons/acre). Additional measurements elsewhere in Puerto Rico confirm these diameter and height growth rates (table 3).

Rooting Habit—María is a deep-rooted species, at least when young. The seedling produces a definite tap root with a quantity of short side roots at regular intervals.

Even on the exposed limestone hills where the soil is too shallow for planting seedlings, roots of maría, once established, penetrate to considerable depths. Planting in shallow soil pockets on lower slopes and bottom lands has given excellent results.

Reaction to Competition—María is intolerant of intense shade in the seedling phase. Seeds below the dense cover of the parent tree may germinate but often become encrusted with mosses and lichens. In contrast, seedlings in full sunlight may suffer from sun scorching in the dry season. Light shade in the first couple of years appears to yield the best growth. After successful establishment, however, full sunlight is needed for most rapid development. Overall, maría is classed as intermediate in tolerance to shade.

In areas subject to drought, weedings may not be needed. In humid areas, circular weeding 1 m (3 ft) around the seedlings should be done at least once a year for 3 years. In an experiment conducted by

Table 2—Mean annual increment and yield for plantation-grown maría (*Calophyllum calaba*) in tropical forests of the Western Hemisphere (*35*)[1]

	Site characteristics			Stand		Mean annual increment				Mean annual yield	
Location	Elevation	Rainfall	Soil	Density	Age	Height	D.b.h.	Volume	Biomass	Volume	Biomass
	m	*mm*		*trees/ha*	*yr*	*m*	*mm*	*m³/ha*	*t/ha*	*m³/ha*	*t/ha*
Trinidad											
Carretera Arena	46	2440	Sandy	620	9	1.2	11	4.33	2.20	0.22	0.11
				304	14	1.1	10	5.29	2.69	1.00	0.52
				185	19	1.0	9	4.95	2.51	1.74	0.90
				NA[2]	31	1.0	11	NA	NA	NA	NA
South Watershed Reserve	35	1650	Sandy	1349	8	1.4	14	5.25	2.67	0.75	0.38
				823	14	1.1	11	7.21	3.68	2.21	1.12
				311	25	0.8	10	7.12	3.63	3.84	1.95
				NA	34	0.6	10	NA	NA	NA	NA
Puerto Rico											
Maricao	630	2670	Serpentine	1297	25	0.7	6	12.60	6.41	7.00	3.56
				1001	33	0.6	7	NA	NA	NA	NA
Luquillo	450	3050	Clay	922	22	0.7	7	NA	NA	NA	NA
	ft	*in*		*trees/acre*	*yr*	*ft*	*in*	*ft³/acre*	*tons/acre*	*ft³/acre*	*tons/acre*
Trinidad											
Carretera Arena	150	96	Sandy	251	9	3.9	0.44	61.86	0.98	3.17	0.05
				123	14	3.6	0.39	75.57	1.20	14.30	0.23
				75	19	3.3	0.37	70.72	1.12	24.80	0.40
				NA	31	3.3	0.43	NA	NA	NA	NA
South Watershed Reserve	110	65	Sandy	546	8	4.6	0.54	75.00	1.19	10.72	0.17
				333	14	3.6	0.42	103.00	1.64	31.63	0.50
				126	25	2.6	0.38	101.72	1.62	54.86	0.87
				NA	34	2.0	0.38	NA	NA	NA	NA
Puerto Rico											
Maricao	2,070	105	Serpentine	525	25	2.3	0.22	180.00	2.86	100.00	1.59
				405	33	2.0	0.28	NA	NA	NA	NA
Luquillo	1,480	120	Clay	373	22	2.3	0.27	NA	NA	NA	NA

[1] Height and diameter values derived from dominant and codominant trees only.
Volume determined outside bark to an upper stem diameter of 10 cm (3.9 in).
Biomass = Volume x 0.51 (specific gravity of Maria) estimate is high because no correction is made for bark thickness.
[2] Not available.

Institute of Tropical Forestry personnel with seedlings planted in *Panicum* spp. and *Ipomoea* spp. undergrowth, the weeded seedlings had 50 percent survival with an average height of 2.3 m (8 ft), but the unweeded trees showed only 12 percent survival and growth to 1.2 m (4 ft).

María has a sturdy stem and its greatest attribute is its ability to dominate grass, ferns, or vines when planted on adverse sites (*21*). Usually close spacings of 1.8 by 1.8 m (6 by 6 ft) or 1.5 by 1.5 m (5 by 5 ft) are used to accelerate crown closure and preclude lateral branching (*20*). Wider spacings yield more rapid diameter increment but create poor tree form.

Attempts to improve growth by thinning have been tried in dense, overstocked 18-year-old stands in Puerto Rico (*34*). The stands were located on infertile serpentine soils in the western Cordillera and had densities ranging from 1,280 to 3,530 stems per hectare (518 to 1,429/acre). The stands were about 10 to 15 m (35 to 50 ft) tall and about 10 cm (4 in) in d.b.h.

Table 3—Mean annual increment for plantation-grown maría (*Calophyllum calaba*) in Puerto Rico (*20,22*)

Location	Site characteristics			Stand	Mean annual increment		
	Elevation	Rainfall	Soil	age	Height	D.b.h.	Basal area
	m	*mm*		*yr*	*m*	*mm*	*m²/ha*
Guajataca	150	2000	Limestone	13	0.2	5.3	0.6
Luquillo	450	2550	Deep clay	13	0.5	7.0	0.8
Luquillo	360	3050	Deep clay	6.5	0.9	8.2	NA
Luquillo	300	2500	Shallow clay	7	0.9	8.7	NA
Luquillo	300	2500	Clay	13	0.7	9.6	NA
	ft	*in*		*yr*	*ft*	*in*	*ft²/acre*
Guajataca	490	79	Limestone	13	0.7	0.21	2.5
Luquillo	1,480	100	Deep clay	13	1.6	0.28	3.8
Luquillo	1,180	120	Deep clay	6.5	3.0	0.32	NA
Luquillo	980	98	Shallow clay	7	3.0	0.34	NA
Luquillo	980	98	Clay	13	2.3	0.38	NA

[1] Not available

Basal areas ranged from 13.3 to 37.9 m²/ha (58 to 165 ft²/acre). The difference in diameter between dominant and suppressed stems was only 2.5 cm (1 in).

In the most dense stand, basal area was reduced from 37.9 m²/ha (165 ft²/acre) to 25.7 m²/ha (112 ft²/acre), but no acceleration in diameter growth was observed after 5 years. A heavier thinning was made on adjacent plots, leaving only 18.4 m²/ha (80 ft²/acre). In this instance, 85 percent of the residual trees had crown freedom and overhead light. After 3 years, no detectable acceleration in diameter growth was evident. Crowns were still narrow, and few new branches were formed (*33*).

Damaging Agents—The heartwood is rated as durable to moderately durable with respect to decay resistance but susceptible to marine borers (*6,8*), the drywood termite (*Cryptotermes brevis*) in Puerto Rico (*18,36*), and the subterranean termites (*Captotermes brevis, Heterotermes convexinotatus, H. tennis,* and *Nasutitermes corniger*) in Panama (*6*). When maría was substituted for imported track sleepers in British Honduras, a marked difference was observed between wet and dry sections of the track. In wet sections, fungal attack was prevalent; in the dry section, termite attack was more pronounced (*24*).

A fast-killing wilt that affects all tree sizes in about the same length of time was observed in Central America (*9*). It is first evidenced by a dry branch in the tree top, followed in 4 weeks by chlorotic foliage, and then death. Internally, dark-brown streaking is observed in the vascular system caused by a gum that plugs the vessels. The causal agent is a species of *Cephalosporium*. The disease was described as the first epidemic disease in Central America and was compared in its virulence to chestnut blight (*Cryphonectria parasitica*), Dutch elm disease (*Ceratocystis ulmi*), or persimmon wilt (*Acremonium diospyri*) of the United States (*32*).

In Trinidad, a leaf curl is prevalent on young plants and may be a response to weather conditions. A thread blight fungus (possibly *Corticium stevensii*) was observed on one estate, and in another area, a few trees were attacked by a root fungus tentatively identified as a species of *Rosellinia*. Trees of large size in Trinidad are usually sound to the base (*23*).

Also in Trinidad, maría is infected by mycorrhizae that are present throughout the root system but not extremely abundant. Similar mycorrhizae have been found in 85 percent of the species in the Trinidad flora including other forest species (*14*).

In Puerto Rico, an unidentified seed borer was observed in Maricao Forest (*11*). More common, however, are splotches on leaves and premature defoliation when thrips (Thripidae) infestation is heavy.

Special Uses

The wood of maría is widely used in the tropics. The heartwood varies from yellowish pink through reddish brown while sapwood is generally lighter in color. The grain is usually interlocked, and the specific gravity ranges from 0.51 to 0.57. The wood is fairly easy to work, rating above average in shaping, sanding, and mortising, and below average in planing, turning, and boring. It is moderately difficult to air-season and shows moderate to severe warp. The sapwood is easily impregnated with preservatives by either pressure or open-tank-bath methods, but the heartwood is extremely resistant to impregnation *(8,17,18)*.

Maria wood is suitable for general construction, flooring, bridge construction, furniture, boat construction, cabinetmaking, shingles, interior construction, agricultural implements, poles, crossties, and handles *(15,25)*. It is a good general utility wood where a fairly strong and moderately durable timber is required. In British Honduras, it was substituted for imported creosoted sleepers but required replacement after 3 or 4 years *(24)*. In Mexico, attempts to use the timber in the veneer and plywood industry were not entirely successful *(26)*.

The tree is also planted for shade along streets and as a windbreak or to protect against salt spray near the ocean. Frequently it is pruned to form a dense hedge along property lines in urban areas *(28)*.

The latex from the trunk has been employed medicinally. The fruits are used as hog-feed, and lamp oil is extracted from the seeds *(15,25)*.

The tree's adaptability to a variety of sites in Puerto Rico has made it popular among soil scientists and foresters for rehabilitation of degraded lands.

Genetics

There is ample debate over the nomenclature of maria. *Calophyllum brasiliense* var. *antillanum* (Britton) Standl. was considered a variety of *C. brasiliense* Camb. *(15)*. The former was also considered synonymous with *C. calaba* Jacq., but not L., as well as with *C. antillanum* Britton and *C. jacquinii* Fawc. & Rendle *(15)*. Later, however, *C. brasiliense* Camb. was replaced by *C. calaba* L.

The "variety" *antillanum* is found in Puerto Rico and the Virgin Islands and ranges from Cuba to Jamaica through the Lesser Antilles to Granada. A closely related species, *Calophyllum lucidum* Benth., or a variety known as galba, grows in Trinidad, Tobago, and British Guiana *(15)*. The timbers are similar in appearance and technical properties and they are marketed under a single trade name *(18)*.

Much work needs to be done on the Guttiferae family and the genus *Calophyllum*. Because the range of this species is extensive, approximately from latitude 23° N. to 20° S., it is likely that other varieties remain to be described, and further changes in nomenclature may be expected.

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Carpinus caroliniana Walt. American Hornbeam

Betulaceae Birch family

F. T. Metzger

American hornbeam *(Carpinus caroliniana)*, also called blue-beech, ironwood, water-beech, or lechillo (Spanish), is a small slow-growing short-lived tree in the understory of eastern mixed hardwood forests. The short, often crooked trunk covered with a smooth slate-gray bark is characteristically ridged, resembling the muscles of a flexed arm. The wood is close-grained, very hard, and heavy but little used because such a small tree is rarely converted into sawed products.

Habitat

Native Range

American hornbeam (figs. 1, 2) is native to most of the eastern United States and extends into Canada in southwest Quebec and southeast Ontario. Its western limit is just beyond the Mississippi River from north-central Minnesota to the Missouri River, where it ranges southwestward into much of the Ozark and Ouachita Mountains and eastern Texas. It grows throughout much of the South but is absent from the Mississippi River bottom land south of Missouri, the lowermost Gulf Coastal Plain, and the southern two-thirds of Florida. Northward along the east coast, it is not found in the New Jersey pine barrens, much of Long Island, Cape Cod, northern and eastern Maine, and the White and Adirondack Mountains. It is found in central and southern Mexico, Guatemala, and western Honduras.

Climate

The climate varies greatly from north to south in this species habitat. Mean annual precipitation ranges from 710 mm (28 in) in Minnesota to 1570 mm (62 in) along the Gulf Coast. Most precipitation occurs during the growing season, April through September. Mean January temperatures range from -13° C (8° F) to 16° C (60° F) and the mean July temperatures range from 16° C (60° F) to 29° C (84° F). Frost-free periods are from 80 to 320 days.

Soils and Topography

Best growth and development of American hornbeam occurs on rich, wet-mesic sites, but it is not restricted to such sites and can tolerate a wide variety of conditions. Habitat requirements and tolerances of the species are similar across its range.

Soils primarily associated with the species are in the orders Alfisols, Ultisols, and Inceptisols but American hornbeam also occurs on Entisols, Spodosols, Histosols, and Mollisols.

The best sites may be characterized as having abundant soil moisture but sufficient drainage to prevent saturation and poor aeration of the soil during the growing season *(4,51)*. Typically, the best sites are alluvial or colluvial soils in the transition zone between mesic and wet areas *(46)*, as near lakes and swamps *(35)*, on well-drained terraces of rivers *(32,45)*, terraces or steep slopes of minor streams with some gradient *(39)*, coves, ravine bottoms *(33)*, and rises in lowlands *(40)*. Surface soil layers are somewhat poorly to well drained but the subsoil may not be as well drained, may have a high fluctuating water table, or may be of heavier texture. Soil water-holding capacity usually is high *(15,49)*. Upper soil horizons are primarily loams or of loam-influenced textures. Nutrients and organic matter tend to accumulate on these sites *(36)*, and calcium and magnesium in particular are normally more abundant than in surrounding soils *(13)*. Soil pH tends to be acidic—normally from 4.0 to 5.6—but can be as high as 7.4 *(35)*.

The species also grows well on wetter sites, such as hardwood swamps on mineral soils or mucks *(3,37)*. The key appears to be improving soil moisture conditions through the growing season because the species is only moderately tolerant of flooding *(14)*. It is eliminated from sites inundated more than 25 percent of the time *(24)*. Accordingly, it is absent or rare on the wettest sites, such as lower floodplain terraces, permanently inundated areas, and swamps with peat soils.

American hornbeam also grows, to a lesser extent, on mesic to xeric sites *(5,19)*. In Florida and Ontario the species occurs more often on dry-mesic than on mesic or xeric sites. The dry-mesic sites in Ontario have a higher soil moisture retaining capacity than the others *(35)*. In hilly terrain it is found most frequently on north aspects but also grows on ridge tops and on south aspects where subirrigation of the site improves soil moisture *(51)*.

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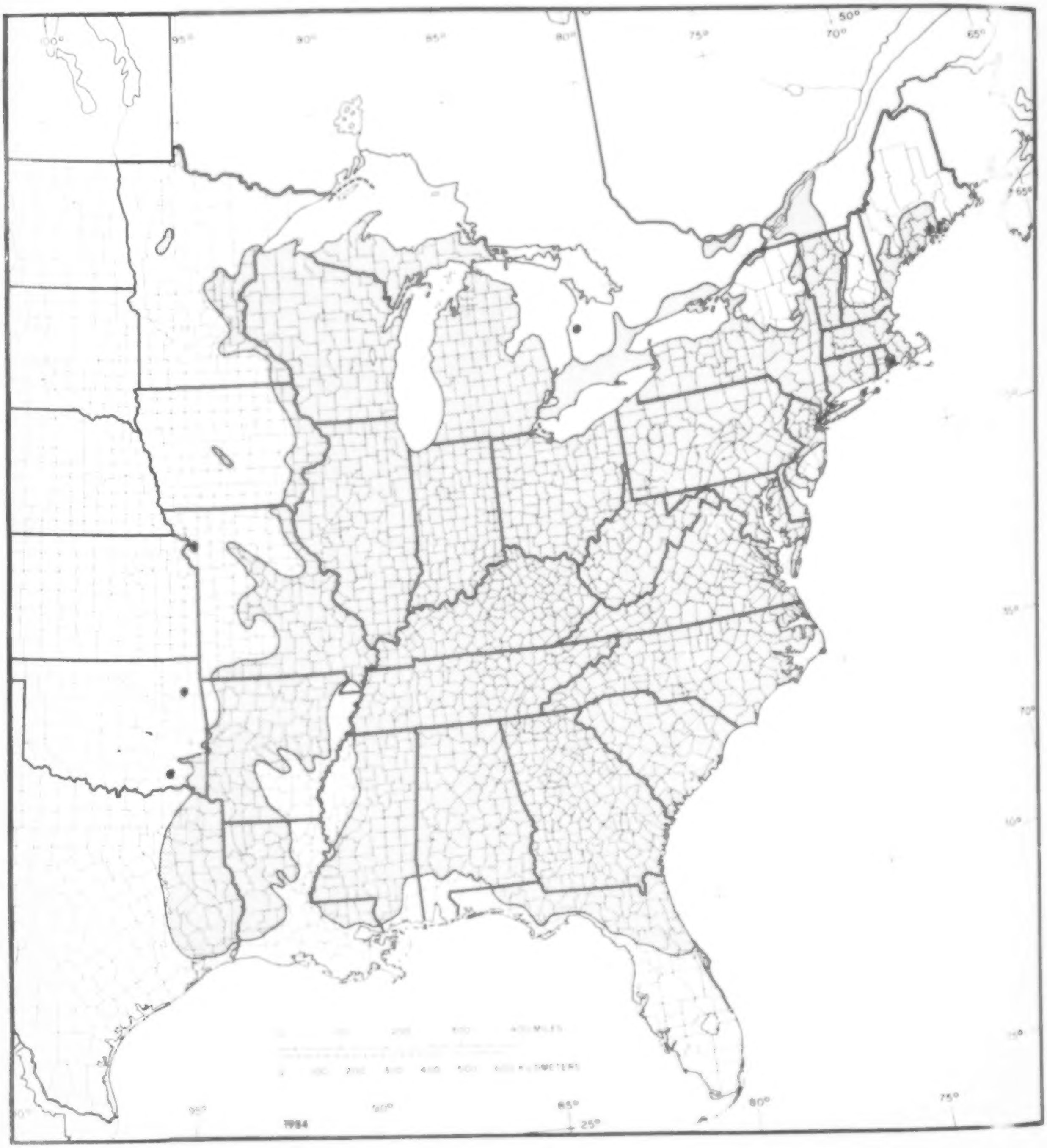
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Figure 1—*The native range of American hornbeam.*

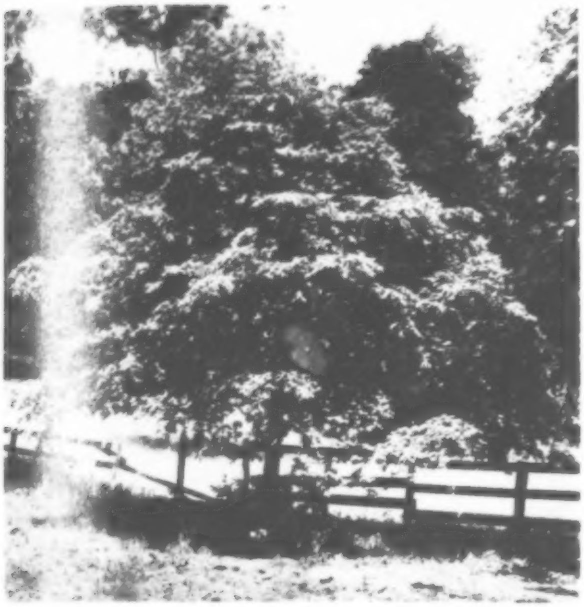

Figure 2—*American hornbeam*

The upper altitudinal limit of American hornbeam is 910 m (3,000 ft) in the Great Smoky Mountains, but it is much more common at about 490 m (1,600 ft) *(59)*.

Concentrations of potassium, nitrogen, calcium, and phosphorus in the foliage of the species are low in comparison to those of other species *(2)*. American hornbeam leaf litter, on the other hand, has high concentrations of these nutrients in relation to other species *(57)*.

Associated Forest Cover

American hornbeam is typically an understory species and only rarely occurs in the overstory or dominates a stand. It is present in the following forest cover types (Society of American Foresters) (22): Northern Forest Region, Black Cherry-Maple (Type 28), Beech-Sugar Maple (Type 60); Central Forest Region, White Oak-Black Oak-Northern Red Oak (Type 52), White Oak (Type 53), Northern Red Oak (Type 55), River Birch-Sycamore (Type 61), Pin Oak-Sweetgum (Type 65); Southern Forest Region, Swamp Chestnut Oak-Cherrybark Oak (Type 91), Sweetgum-Yellow-Poplar (Type 87).

American hornbeam is found in a wide variety of forest communities and with many tree species because its habitat frequently is an ecotone in which species from wet and mesic sites intergrade. In the North, it is a minor component of many different types, infrequently becoming the first or second most abundant tree species in the subcanopy layer *(32)*. It is associated with northern hardwoods and their wet site variants. Sugar maple *(Acer saccharum)* and/or American beech *(Fagus grandifolia)* are dominant in many situations but may be replaced by eastern hemlock *(Tsuga canadensis)*, yellow birch *(Betula alleghaniensis)*, red maple *(Acer rubrum)*, American elm *(Ulmus americana)*, silver maple *(Acer saccharinum)*, and black ash *(Fraxinus nigra)* on wetter sites.

In the central portion of its range, American hornbeam also is a minor component of stands. Species dominant in northern stands also dominate here along with white *(Quercus alba)*, black *(Q. velutina)*, northern red *(Q. rubra)*, scarlet *(Q. coccinea)*, pin *(Q. palustris)*, and chinkapin *(Q. muehlenbergii)* oak; bitternut hickory *(Carya cordiformis)*; black tupelo *(Nyssa sylvatica)*; sweetgum *(Liquidambar styraciflua)*; yellow-poplar *(Liriodendron tulipifera)*; river birch *(Betula nigra)*; and basswood *(Tilia americana)*.

The species attains its greatest prominence in southern stands, yet remains a member of the understory. In a number of areas it is the most numerous of all tree species in the stand *(36,40)*. It is found in southern mixed hardwood and loblolly pine *(Pinus taeda)* forests. Overstory species that frequently dominate these stands are sweetgum, water *(Quercus nigra)*, white, laurel *(Q. laurifolia)*, willow *(Q. phellos)*, cherrybark *(Q. falcata* var. *pagodifolia)*, and swamp chestnut *(Q. prinus)* oak, American beech, black tupelo, red maple, loblolly pine, southern magnolia *(Magnolia grandiflora)*, and yellow-poplar.

The species is also an important member of some nonforest vegetative types in the Northeast. It is an early migrant and forms pure stands in moist old fields *(61)* and grows in persistent shrub communities in old pastures on hilltops and more exposed hilltops *(20)*.

Understory tree species associated with American hornbeam throughout much of its range include eastern hophornbeam *(Ostrya virginiana)*, flowering dogwood *(Cornus florida)*, witch-hazel *(Hamamelis virginiana)*, the serviceberries *(Amelanchier* spp.), and speckled alder *(Alnus rugosa)*. Northern associates are striped *(Acer pensylvanicum)* and mountain maple *(A. spicatum)*. Red mulberry *(Morus rubra)*, pawpaw *(Asimina triloba)*, and eastern redbud *(Cercis canadensis)* are common associates from the Central States southward. In the South, associated species include sourwood *(Oxydendrum arboreum)*, possumhaw *(Ilex decidua)*, American holly *(Ilex* *opaca*), winged elm (*Ulmus alata*), sweetbay (*Magnolia virginiana*), water-elm (*Planera aquatica*), parsley hawthorn (*Crataegus marshallii*), riverflat hawthorn (*C. opaca*), common persimmon (*Diospyros virginiana*), and Carolina laurelcherry (*Prunus caroliniana*).

Shrub species associated with American hornbeam throughout its range include spicebush (*Lindera benzoin*) and southern arrowwood (*Viburnum dentatum*). In the northern half of its range, American hornbeam is associated with mapleleaf viburnum (*Viburnum acerifolium*), redberry elder (*Sambucus pubens*), common winterberry (*Ilex verticillata*), and alternate-leaf dogwood (*Cornus alternifolia*). In the southern half of its range it is associated with devils-walkingstick (*Aralia spinosa*), beautyberry (*Callicarpa americana*), Virginia-willow (*Itea virginica*), southern bayberry (*Myrica cerifera*), sweetleaf (*Symplocos tinctoria*), and tree sparkleberry (*Vaccinium arboreum*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—The species is monoecious, with male and female catkins borne separately on the same tree and first appearing in the spring concurrently with leaf-out. Catkins are green to brown with red on the scales. Staminate catkins are pendant from lateral, short branches and 3 to 4 cm (1.25 to 1.5 in) long. Pollen matures and is wind disseminated in the spring (*63*). Pistillate catkins are 13 to 19 mm (0.5 to 0.75 in) long and occur in spikelike groups at the terminus of leafy shoots. Flowering occurs between March 20 and May 6 in the Southeast and during April through May in the North.

Seed Production and Dissemination—The fruit is an ovoid, ribbed, 5 to 8 mm (0.2 to 0.3 in) long nutlet. It matures in one season, changing from green to light-greenish-brown or brown on maturity. The nutlet is borne at the base of a distinctive three-lobed involucre, about 2.5 cm (1 in) long; these occur in clusters 5 to 10 cm (2 to 4 in) long. The averages reported for nutlets per kilogram range from 66,000 to 88,000 (30,000 to 40,000/lb), while the range is between 33,000 and 143,000 (15,000 and 65,000/lb) (*48,62*). Large seed crops occur at 3- to 5-year intervals. Seeds are primarily dispersed by birds but are also dispersed short distances by wind. Germination is epigeal. Germination capacity of stratified seed is low—usually less than 60 percent and occasionally as low as 1 to 5 percent—but 100 percent germination was obtained using immature green seed (*54*). Dormancy occurs in both the embryo and endosperm (*48*). Stratification at 4° C (40° F) for 18 weeks, stratification plus gibberellic acid treatment, and scarification of the seed coat plus gibberellic acid treatment all improve germination (*9*).

Seedling Development—The types of seedbeds and environments favorable to establishment under natural conditions has to be surmised from nursery experience and the habitat preference of established plants. The optimum nursery seedbed has soils that are rich, loamy, and continuously moist and the site is free of extreme environmental change (*48*). This approximates natural conditions where the species is most frequently found. Abundant natural reproduction in undisturbed forests indicates the species ability to become established on leaf litter seedbeds under deep shade and with competition from other species (*12,50*). The species also becomes established on sites that are wetter and drier than optimum, as well as on open sites.

American hornbeam responds well to various degrees of overstory removal in regeneration harvests. In two hardwood seed-tree harvest areas in southeastern Arkansas, the proportion of American hornbeam in the reproduction increased during the 18 years after cutting (*30*). Regeneration of the species consisted of advance reproduction, new seedlings, stump sprouts, and root suckers. Sprouts grew from 1.2 to 1.5 m (4 to 5 ft) in the first year. By the 18th year, American hornbeam was becoming subordinate in diameter to sweetgum and the red oaks. The species also responded well to release after clear-cutting hemlock-hardwoods in southern New England (*34*). However, density and basal area stocking of American hornbeam in relation to other species were unaffected after a partial harvest of a pine-hardwood stand in Louisiana (*6*).

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—American hornbeam is unsuited for commercial timber production because it is usually small, twisted, and multi-stemmed. In undisturbed stands, from 70 to 93 percent of the American hornbeam were saplings less than 13 cm (5 in) d.b.h. and less than 1 percent were 25 cm (10 in) d.b.h. or larger (*21,40*), which is a common minimum diameter for saw logs. Heights of mature individuals generally range from 5 to 6 m (15 to 20 ft) in Canada and from 8 to 11 m (25 to 35 ft) in the South. Th largest individual was found in New York. It has a diameter of 70 cm (27 in), a height of 20 m (65 ft), and a crown spread of 20 m (66 ft) *(29)*.

Rooting Habit—No information available.

Reaction to Competition—American horn beam is a very shade-tolerant species, capable of persisting in the understories of late seral and climax communities. Tolerance is greatest among seedlings and declines as the trees age, requiring an opening in the canopy for the species to reach maturity. It is one of a few species in both northern and southern forests whose abundant reproduction assures its replacement in stands across a wide spectrum of sites *(27,55)*. This is evidenced by an inverse-J-shaped diameter distribution for the species in many stands. On certain southern sites the species is so aggressive that it will replace overstory species lost through logging or catastrophe and prevent larger species from reproducing *(17,30)*.

Ecologists consider American hornbeam a member of near-climax to climax communities. In Wisconsin where climax species are assigned a climax adaptation number of 10, American hornbeam is rated 7 and 8 on uplands and 8 and 9 on lowlands for the northern and southern parts of the State, respectively *(16)*. Similarly the species is rated 7 in New Jersey *(11)*. It is ranked fifth highest among 79 Central States species on the basis of a multivariate analysis of various species characteristics that favor establishment and growth under climax forest conditions *(58)*.

American hornbeam first appeared in seral communities developing on old fields about 12 to 18 years after the sites were abandoned in North Carolina *(41)* and about 25 to 40 years after the sites were abandoned in New Jersey *(26)*. It enters these communities as a minor component when a sapling-size tree-shrub community is dominant. In much older stands in North Carolina it is more abundant. In maturing second-growth hardwood stands in Connecticut, hornbeam had initially been an important species, the most abundant one, in fact, on moist sites. But, over a 50-year period it declined in density, basal area, and ingrowth, eventually becoming a minor component of all stands *(53)*.

In forests managed for commercial timber production, American hornbeam is considered a weed and is discriminated against in stand improvement. Although hornbeam is considered difficult to kill, herbicides have been effective. Mistblowing a mixture of 2,4-D and 2,4,5-T and injecting 2,4-D, Tordon 101, and Tordon 144 have killed 90 percent or more of the trees *(13,44)*. Prescribed burning is used to control the understory hardwoods, including American hornbeam, that become established under southern pines.

Damaging Agents—Insect and disease damage is not a serious problem with American hornbeam. The species is resistant to frost damage; its succulent foliage can withstand temperatures as low as -8.5° C (17° F) *(1)*. The tree is very windfirm. Recreational use in forested campgrounds disposes it to increased disease infection, insect infestation and decline; it is the tree least capable of withstanding such use of the 22 hardwood species evaluated *(47)*.

American hornbean is susceptible to fire. Wildfires severe enough to kill the hardwood component of white oak stands in Rhode Island eliminated American hornbeam *(10)*. Normally, the species made up 6 percent of the understory stems. However, neither a crown fire nor a ground fire affected the status of American hornbeam in the ninth year after burning a loblolly pine stand in North Carolina *(42)*.

Special Uses

American hornbeam is an important food of gray squirrels in southern bottom-land hardwoods; otherwise it is of secondary importance to wildlife *(25)*. Seeds, buds, or catkins are eaten by a number of songbirds, ruffed grouse, ring-necked pheasants, bobwhite, turkey, and fox and gray squirrels. Leaves, twigs, and larger stems are consumed by cottontails, beaver, and white-tailed deer *(18,25)*.

Reproduction is browsed by white-tailed deer throughout the species range but it is not a preferred food *(7,28)*. The species is heavily used by beaver because it is readily available in typical beaver habitat *(38)*.

The orange and scarlet coloration in the fall make this an attractive ornamental tree. It is not widely used, however, because it is difficult to transplant and does not do well on exposed sites *(60)*.

The wood of American hornbeam is not important in commerce because the tree is too small, but its tough, dense, and close-grained wood is used for tool handles, levers, wedges, and mallets.

Genetics

An American hornbeam, variety *virginiana*, is recognized by some authorities but its validity is questionable. It replaces the typical form in the northern half of the species range with some overlapping in the Central States. The two forms are separated by features of the bract of the fruiting

best copy available

ament and the leaves, but in Ohio the two characteristics do not necessarily vary at the same time, resulting in confusion *(8)*.

American hornbeam exhibits clines (from north to south) in several physiological and morphological properties. Fruit weights increase northward *(62)*; the length of cold preconditioning required for bud bursting varies latitudinally *(56)*, and the specific gravity of the wood is higher for trees growing north of latitude 36° N. than for trees growing at latitudes 31° to 36° N. *(55)*.

The species has eight pairs of chromosomes *(63)*.

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Carya aquatica (Michx. f.) Nutt. Water Hickory

Juglandaceae **Walnut family**

John K. Francis

Water hickory (*Carya aquatica*) is a major constituent of clay flats and backwater areas near streams and rivers of the South. Also known as bitter pecan, the species reproduces aggressively from both seed and sprouts. Cutting practices that suppressed competing species have allowed it to increase in better drained areas. Because of "shake" and smaller size, water hickory is deemed inferior to pecan (*C. illinoensis*) for sawing. Water hickory is a major component of wetland forests now considered important in cleansing drainage waters.

Habitat

Native Range

Water hickory (figs. 1, 2) inhabits the Atlantic and Gulf Coastal Plains from southeastern Virginia to

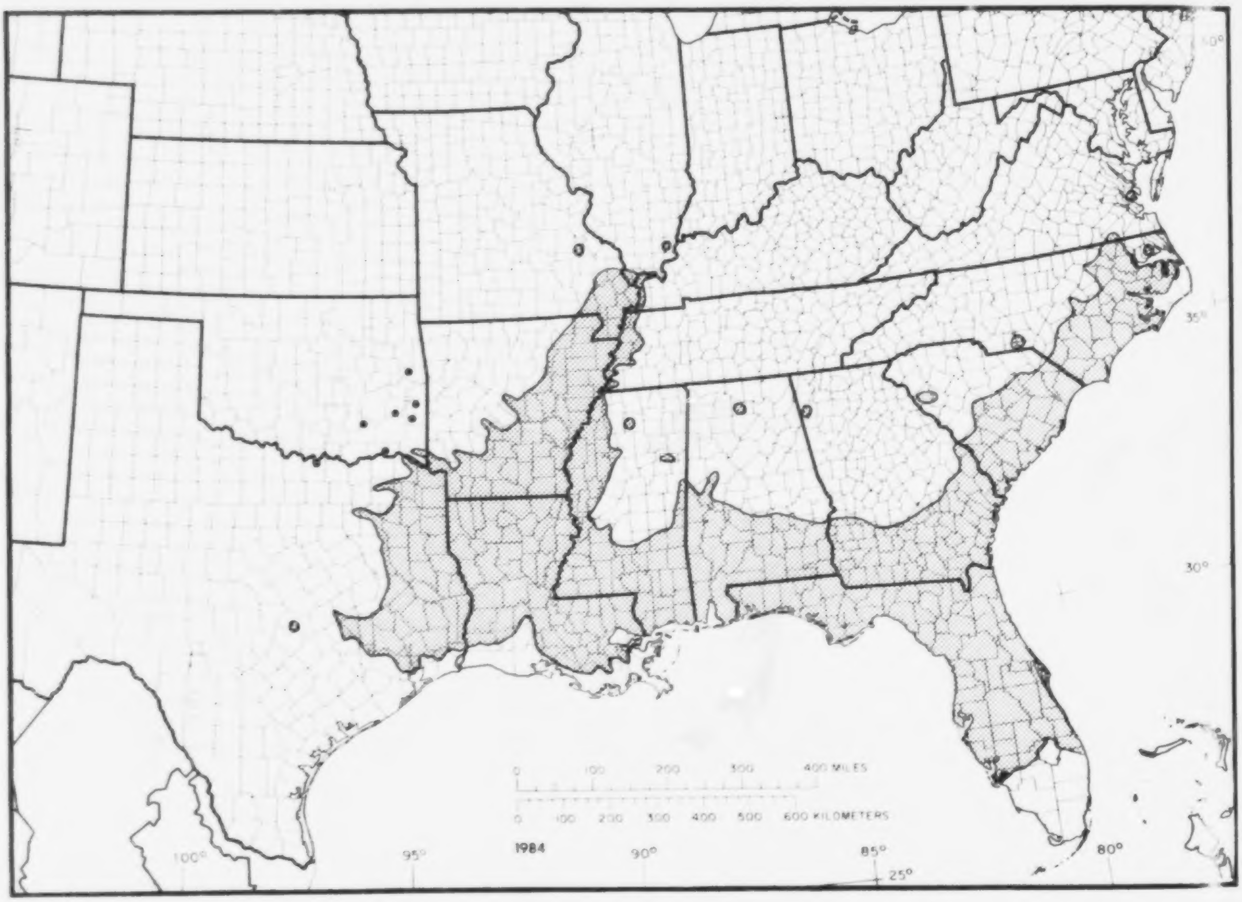

Figure 1—*The native range of water hickory.*

The author is Soil Scientist, Southern Forest Experiment Station, New Orleans, LA. (Research on this species was done in cooperation with the University of Puerto Rico, Rio Piedras.)

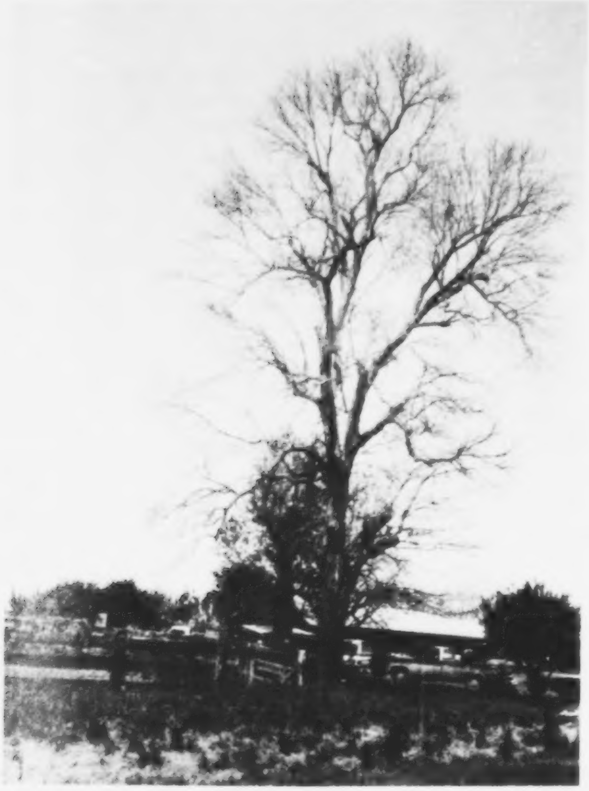

Figure 2—*Open-grown water hickory in a yard in Chicot County, AR.*

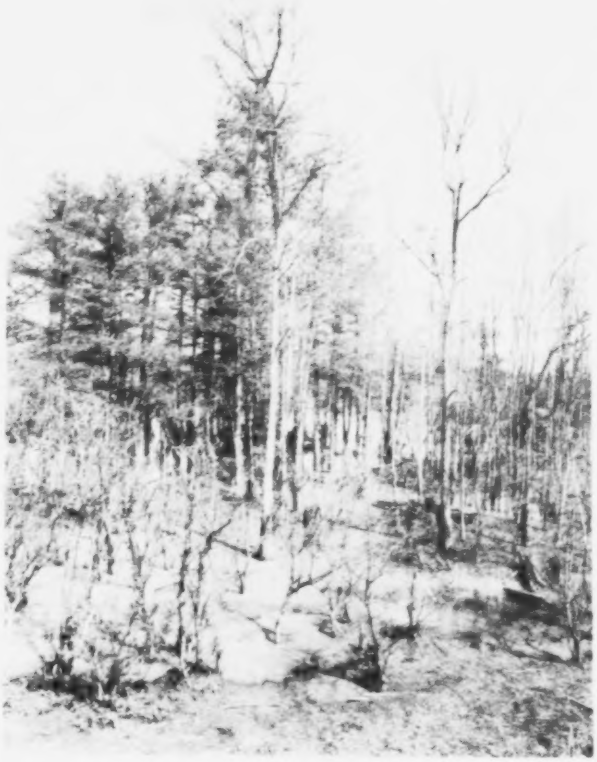

Figure 3—*Young water hickory in an overflow area of a bayou in Chicot County, AR.*

southern Florida, west into eastern Texas, and the Mississippi Valley north to southern Illinois *(5)*.

Climate

Water hickory grows in a warm, humid climate throughout its range. The average annual precipitation varies from 1020 to 1520 mm (40 to 60 in). A mean rainfall of 640 mm (25 in) occurs during the April through September growing season. The mean January temperature is 2° to 16° C (35° to 60° F); mean July temperature, about 27° C (80° F); and an average frost-free period of 200 to 300 days.

Soils and Topography

Water hickory attains its best growth on moist but well-drained loamy or silty soils in the Mississippi River Valley and along some Coastal Plain streams. However, because of its slow growth rates, it is rare on these sites except where it has been favored by repeated "high-grade" logging *(5)*. Water hickory more commonly occupies wet sites where only a few species of hardwoods survive (fig. 3). It is common on clay flats, sloughs, and backwater areas, but seldom in coastal swamps or sites where soils are continually saturated. The species is most common on soils in the Vertic Haplaquepts subgroup of the order Inceptisols. Water hickory sites are subject to inundation during heavy rains and stream overflow, as well as severe drying with cracking of the soil during occasional dry summers.

Associated Forest Cover

Water hickory is a major component of two forest cover types: Sugarberry–American Elm–Green Ash (Society of American Foresters Type 93) and Overcup Oak–Water Hickory (Type 96). It is a minor component in Sweetgum–Willow Oak (Type 92) and is sometimes found on the edge of Baldcypress (Type 101) and Baldcypress–Tupelo (Type 102) *(2)*.

Important associated tree species are overcup, Nuttall, and willow oaks *(Quercus lyrata, Q. nuttallii,* and *Q. phellos)*; cedar and American elms *(Ulmus crassifolia* and *U. americana)*; waterlocust and honeylocust *(Gleditsia aquatica* and *G. triacanthos)*; pecan; green ash *(Fraxinus pennsylvanica)*; sugarberry *(Celtis laevigata)*; persimmon *(Diospyros virginiana)*; red maple *(Acer rubrum)*; and baldcypress *(Taxodium distichum)*.

The most frequent noncommercial trees and shrubs associated with water hickory are hawthorn *(Crataegus* spp.), swamp-privet *(Forestiera acuminata)*, roughleaf dogwood *(Cornus drummondii)*, buttonbush *(Cephalanthus occidentalis)*, possumhaw *(Ilex decidua)*, and water-elm *(Planera aquatica)*.

Life History

Reproduction and Early Growth

Water hickory regenerates aggressively from seeds and sprouts. Seeds germinate and become established on disturbed soil or understory duff. To develop, understory seedlings must be released. Many of our present stands of water hickory, especially on imperfectly drained flats, have been regenerated and released by heavy preferential logging of more valuable species. On poorly drained sites, where competition is not so intense, water hickory grows to fill openings created by windthrow and natural mortality as well as logging.

Flowering and Fruiting—Water hickory is monoecious. Male and female flowers appear during April and May, while the leaves are developing. The male flowers are in stalked catkins on branches of the current or previous year, and the female flowers are in short spikes or stalks. The fruit, covered by a thin husk during development, are thin-shelled, flattened, and have a bitter seed. Nuts fall between October and December of the same year.

Seed Production and Dissemination—Seed production begins when the trees are about 20 years old, or about 20 cm (8 in) in d.b.h. *(9)*. Optimum seed-bearing age is from 40 to 75 years, or after the trees reach 51 cm (20 in) in d.b.h. Heavy seed crops are produced in most years, and a thrifty tree may produce up to 70 liters (2 bu) of seeds. There are approximately 440 cleaned seeds per kilogram (200/lb). The seeds are disseminated by water and animals; floodwaters are particularly important in carrying seed to new areas.

Seedling Development—After seedfall in the autumn, the seeds lie dormant until germination in late April through early June. Rarely do they remain viable until the second spring. Germination is hypogeal. Sometimes nearly 80 percent of the seed crop germinates *(6)*. As a result, thickets and clumps of water hickory are not unusual. The species is tolerant enough to survive in the understory for at least 15 years, but full sunlight is necessary for development into trees *(4)*. The relatively slow height growth of water hickory requires that it have near freedom from competition to establish itself in the overstory. Because of their extended dormant season, water hickory seedlings are able to survive late-spring floods better than most of their would-be competitors.

Vegetative Reproduction—Stumps less than 61 cm (24 in) and severed roots of water hickory readily sprout. Sprouts grow three or four times faster than seedlings during the first year or two. Even on poorly drained clay soil, first-year sprouts sometimes are 1.5 m (5 ft) tall. Sprouts 4.6 m (15 ft) tall at 5 years have been reported.

Sapling and Pole Stages to Maturity

Growth and Yield—Water hickory on a good site may reach 33.5 m (110 ft) tall and 91 cm (36 in) in diameter *(6)*, with about 16 m (52 ft) of merchantable bole. The tall straight trunk is topped by slender to moderately stout ascending branches. Diameter growth of water hickory is slow for southern species, 2 to 8 mm (0.08 to 0.31 in) per year. At 50 years, dominants might average 35 cm (14 in) in d.b.h. on good sites and only 25 cm (10 in) on poor sites. Site index at base age 50 years ranges between 20 and 29 m (65 and 95 ft). Slow growth rates are typical of water hickory in competition with oaks, sugarberry, gum, and other species on good sites.

Maximum mean annual production of a pure stand (found rarely) on a good site has been established at 10.5 m^3/ha (150 ft^3/acre) *(7)*. Maximum mean annual production on medium and poor sites was estimated at 7.0 m^3/ha (100 ft^3/acre) and 3.5 m^3/ha (50 ft^3/acre), respectively. An average water hickory site might realistically yield 210 m^3/ha (3,000 ft^3/acre) at maturity. Slow growth and poor sites usually keep yields low.

Rooting Habit—Water hickory, like other hickories, grows a taproot in the seedling stage. The wet clayey soils where water hickory usually is found restricts the entire root system to fairly shallow depths. The taproot eventually becomes the source of a coarse, widespreading but shallow lateral root system. The taproot of a 30-cm (12-in) individual, excavated on moderately well-drained clayey soil, ended abruptly with three large lateral roots growing out at right angles. Only a few fine roots extended deeper than 50 cm (20 in).

Reaction to Competition—Water hickory is classed as intermediate in shade tolerance. Owing to its slow growth, poor quality, and consequent low value, most silvicultural operations are intended to favor species other than water hickory. Much "high-grade" logging has made the species more abundant and widespread than it would have been naturally. Water hickory responds well to release. On better drained sites, cutting or deadening all stems above 5 cm (2 in) in d.b.h. should relegate water hickory to a minor position in the future stand. Many seedlings and sprouts may emerge, but most of these are eventually overtopped by faster growing species. In the Overcup Oak–Water Hickory cover type, any kind of harvest will probably result in a major component of water hickory in the future stand. Water control projects that prolong spring flooding tend to favor water hickory.

Damaging Agents—Water hickory is occasionally damaged by insects. Of several borers that attack water hickory, the living-hickory borer, *Goes pulcher*, is the most common *(10)*. Borer attacks most often occur on young trees up to 14 cm (5.5 in) in diameter. Trunks weakened by tunnels sometimes break, and logs formerly infested by borers are of low value. Although this borer is widely distributed, damaging populations are rather local. Leaf-eating insects, especially the forest tent caterpillar, *Malacosoma disstria*, occasionally defoliate trees.

Diseases are ordinarily unimportant to water hickory. Butt and stem rots entering through wounds from fire or logging can be a major source of cull. Heart-rot fungi tend to spread faster in the trunks of this species than in associated oaks and other bottom-land hardwoods *(3)*.

The major defect of water hickory is "shake," found especially in trees on waterlogged sites; yellow-bellied sapsuckers also cause defects. Water hickory tends to support more mistletoe *(Phoradendron serotinum)* than any of its associated species.

Special Uses

The nuts of water hickory are used to a limited extent by squirrels, feral hogs, and other wildlife. Water hickory is occasionally planted or retained in natural stands for a shade tree. The wood is a locally preferred firewood.

Low floodplains, in which water hickory is a dominant species, are being increasingly recognized for their ability to cleanse drainage water and provide refuge for many threatened species of plants and animals.

Genetics

No races have been recorded; population and geographic variations have not been studied except for the hybrid *Carya × lecontei* Little *(C. aquatica × illinoensis)*. This hybrid is fairly common where the range of the two parent species overlaps *(8)*. One other hybrid is recognized, *C. × ludoviciana* (Ashe) Little *(C. aquatica × texana) (1)*.

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Carya cordiformis (Wangenh.) K. Koch **Bitternut Hickory**

Juglandaceae **Walnut family**

H. Clay Smith

Bitternut hickory *(Carya cordiformis)*, also called bitternut, swamp hickory, and pignut hickory, is a large pecan hickory with commercial stands located mostly north of the other pecan hickories.

Bitternut hickory is cut and sold in mixture with the true hickories. It is the shortest lived of the hickories, living to about 200 years. The dark brown close-grained hardwood is highly shock resistant which makes it excellent for tools. It also makes good fuel wood and is planted as an ornamental.

Habitat

Native Range

Bitternut hickory (figs. 1, 2) is probably the most abundant and most uniformly distributed of all the hickories. It grows throughout the eastern United States from southwestern New Hampshire, Vermont, Maine, and southern Quebec; west to southern Ontario, central Michigan, and northern Minnesota; south to eastern Texas; and east to northwestern Florida and Georgia. It is most common, however, from southern New England west to Iowa and from southern Michigan south to Kentucky *(6,23,26)*.

Climate

Throughout the range of bitternut hickory, the mean annual precipitation ranges from 640 to 1270 mm (25 to 50 in) except for a small area in the southern Appalachians where about 2030 mm (80 in) is common. In the northern part of the range, snowfall averages 203 cm (80 in) per year, but in the southern extreme of the range, it rarely snows. During the growing season, from April to September, the precipitation ranges from 510 to 1020 mm (20 to 40 in).

Annual temperatures range from about 4° to 18° C (40° to 65° F), July temperatures from about 18° to 27° C (65° to 80° F), and January temperatures from -15° to 12° C (5° to 54° F). Extremes of 46° to -40° C (115° to -40° F) have occurred within the range. Bitternut seldom grows in areas where the growing season is less than 120 or more than 240 days long *(30,34)*.

Soils and Topography

Bitternut hickory grows in moist mountain valleys along streambanks and in swamps. Although it is usually found on wet bottom lands, it grows on dry sites and also grows well on poor soils low in nutrients *(10)*.

In the northern part of its range, bitternut hickory is found on a variety of sites. It grows on rich, loamy, gravelly soil in low wet woods, and along the borders of streams in Michigan, but it is also found on dry uplands. In the southern part of its range, bitternut is more restricted to moist sites. It reaches its largest size on the rich bottom lands of the lower Ohio River Basin. In the southeastern part of its range, bitternut grows on overflow bottom land, but in its southwestern range, it is common on poor, dry, gravelly upland soils. Bitternut is not found in the mountain forests of northern New England and New York, nor at higher elevations in the Appalachians *(23)*.

Bitternut hickory grows primarily on Ultisols that occupy about 50 percent of its geographic range *(33)*. These soils are low in nutrients and are found primarily in the southern to mid-Atlantic region on gentle to steep slopes. Along the mid-Atlantic, southern, and western ranges, bitternut hickory grows on a variety of soils on slopes of 25 percent or less, including combinations of fine to coarse loams and well-drained quartz sands. On slopes steeper than 25 percent, bitternut hickory grows on coarse loams.

Inceptisols occupy about 15 percent of the bitternut hickory range, dominating the Appalachian portion of the geographic range. On gently to moderately sloped topography, the hickories are found on fine loams with a fragipan. On steep slopes, they are more commonly found on coarse loams. These soils are moderate to high in nutrients and water is available to plants during more than half of the year or more than 3 consecutive months during the warm season.

Mollisols occupy an estimated 20 percent of the bitternut hickory range primarily in western areas *(33)*. These soils typically have a dark, deep, fertile surface horizon more than 25 cm (10 in) thick. Mollisols form under grass in climates that have moderate seasonal precipitation. Bitternut grows on a variety of soil combinations such as wet, fine loams, and sandy-textured soils that often have been burned, plowed, and pastured.

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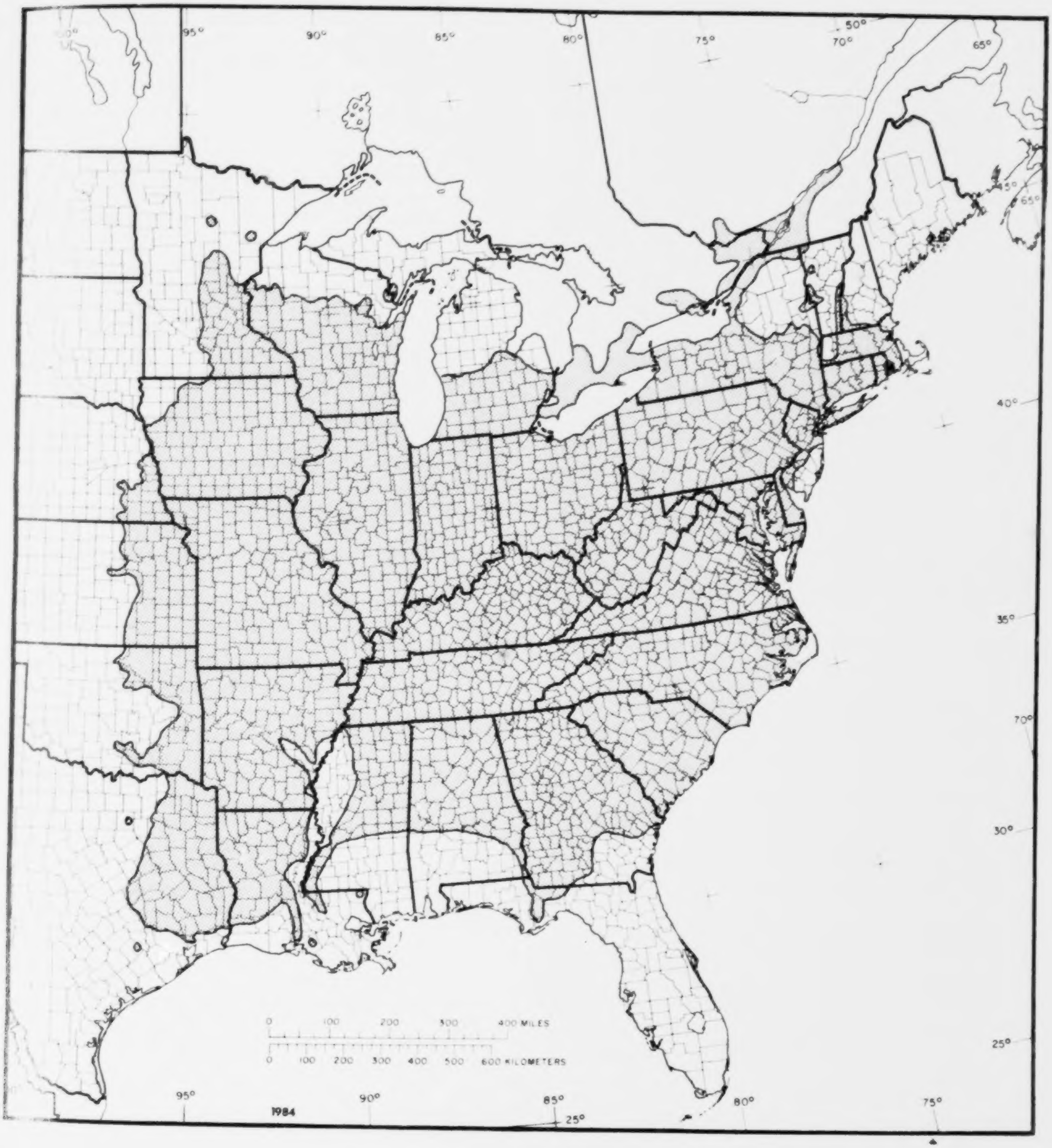
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Figure 1—*The native range of bitternut hickory.*

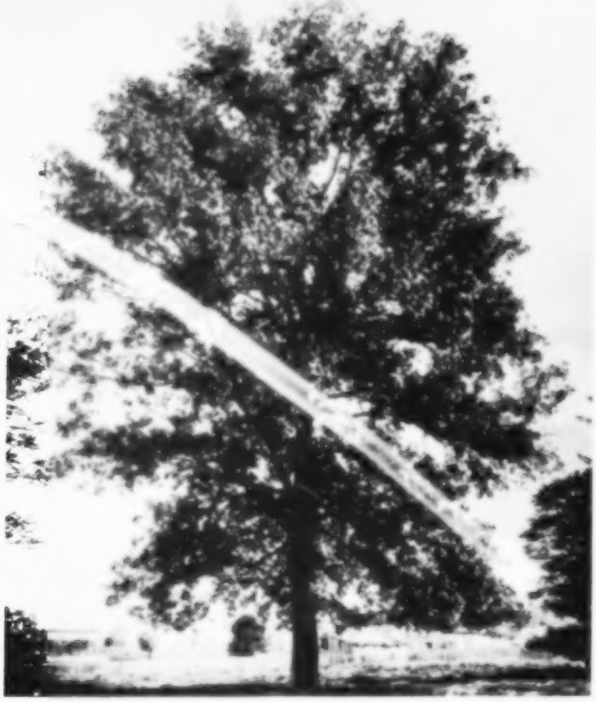

Figure 2—*Typical form of open-grown bitternut hickory.*

Alfisols comprise about 15 percent of the bitternut range, mainly in northern and northwestern portions. These soils contain a medium to high supply of nutrients. In Minnesota and Wisconsin, bitternut hickory is found on moist, well-drained, sandy soils with slopes up to 25 percent. Near Lake Erie and in southern Illinois and northeastern Missouri, it occasionally occurs on wet to moist, poorly drained soils on slopes of less than 10 percent.

Associated Forest Cover

Bitternut hickory, though present throughout the eastern forest, does not grow in sufficient numbers to be included as a titled species in the Society of American Foresters forest cover types *(8)*, but it is mentioned as an associated species in six types. With one exception, most of these types are subclimax to climax.

In the northern forest region, the types are Sugar Maple-Basswood (Society of American Foresters Type 26) and Sugar Maple (Type 27); in the central forest region, White Oak-Black Oak-Northern Red Oak (Type 52) and White Oak (Type 53); in the southern forest region, Loblolly Pine-Shortleaf Pine (Type 80) and Swamp Chestnut Oak-Cherrybark Oak (Type 91). Hickories are mentioned, but not individually identified, in 16 other cover types; however, 5 of these mentioned types are subclimax to climax.

Because bitternut hickory occupies many sites throughout its geographic range, its associations vary. In addition to the species named in the cover types, bitternut hickory grows with various oaks *(Quercus* spp.) in the northern region. In the southern part of Quebec, there is a sugar maple-bitternut hickory subtype that is restricted to deep soils. Trees associated with it include basswood *(Tilia* spp.), eastern hophornbeam *(Ostrya virginiana)*, northern red oak *(Quercus rubra)*, butternut *(Juglans cinerea)*, and black maple *(Acer nigrum)*. In the central hardwood region, extending in to northwestern Minnesota, bitternut hickory is found with hackberry *(Celtis occidentalis)*, green ash *(Fraxinus pennsylvanica)*, and butternut. Common understory herbaceous stems include largeflower bellwort *(Uvularia grandiflora)*, Virginia creeper *(Parthenocissus quinquefolia)*, hepatica *(Hepatica acutiloba)*, wood-nettle *(Laportea canadensis)*, wild ginger *(Asarum canadense)*, large flowering trillium *(Trillium grandiflorum)*, springbeauty *(Claytonia caroliniana)*, violets *(Viola* spp.), anemone *(Anemone* spp.), Solomons-seal *(Polygonatum pubescens)*, and false Solomons-seal *(Smilacina stellata)*.

In upland oak types of the central forest region, bitternut hickory is commonly associated with mockernut hickory *(C. tomentosa)*, pignut hickory *(C. glabra)*, and shagbark hickory *(C. ovata)*. Other common associates are yellow-poplar *(Liriodendron tulipifera)*, blackgum *(Nyssa sylvatica)*, white ash *(Fraxinus americana)*, green ash, maples, elms *(Ulmus* spp.), pines *(Pinus* spp.), and eastern hemlock *(Tsuga canadensis)*. Important understory trees and shrubs associated with bitternut include dogwood *(Cornus* spp.), sassafras *(Sassafras albidum)*, sourwood *(Oxydendrum arboreum)*, downy serviceberry *(Amelanchier arborea)*, redbud *(Cercis canadensis)*, American hornbeam *(Carpinus caroliniana)*, eastern hophornbeam *(Ostrya virginiana)*, witch-hazel *(Hamamelis virginiana)*, sumac *(Rhus* spp.), viburnums *(Viburnum* spp.), rhododendron *(Rhododendron maximum)*, wild grape *(Vitis* spp.), greenbriers *(Smilax* spp.), Virginia creeper, and poison-ivy *(Toxicodendron radicans)*. Bitternut hickory is also prominent in the southern bottom-land hardwood swamps, in the cover type Chestnut Oak-Cherrybark Oak. There it is found with shellbark hickory *(C. laciniosa)*, shagbark and mockernut hickories, green and white ash, white oak *(Quercus alba)*, Shumard oak *(Q. shumardii)*, Delta post oak (*Q. stellata* var. *paludosa*), and blackgum. Understory vegetation in this area includes pawpaw (*Asimina triloba*), American hornbeam, flowering dogwood, painted buckeye (*Aesculus sylvatica*), devils-walkingstick (*Aralia spinosa*), redbud, American holly (*Ilex opaca*), dwarf palmetto (*Sabal minor*), southern arrowwood (*Viburnum dentatum*), and possumhaw (*Ilex decidua*).

In the southern pine forest region, bitternut hickory is found primarily as an understory species on dry open sites where shortleaf pine (*Pinus echinata*) predominates along with blackjack oak (*Quercus marilandica*), post oak, mockernut hickory, pignut hickory, and flowering dogwood. Vines, herbaceous vegetation, and shrubs are sparse. The most common understory vegetation includes hawthorns (*Crataegus* spp.), beautyberry (*Callicarpa americana*), blueberry (*Vaccinum* spp.), sumacs, longleaf uniola (*Uniola sessiflora*), panicums (*Panicum* spp.), sedges (*Carex* spp.), and bluestems (*Andropogon* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Bitternut hickory is monoecious; male and female flowers are produced on the same tree. The male flowers are in catkins about 8 to 10 cm (3 to 4 in) long and are produced on branches from axils of leaves of the previous season or from the inner scales of the terminal bud at the base of the current growth. Female flowers are about 13 mm (0.5 in) long and appear in short spikes on peduncles terminating in shoots of the current year (*3*). Depending on latitude and weather, greenish flowers bloom in the spring from April to May. Usually the male flowers emerge before the female flowers. Hickories produce very large amounts of pollen that are carried by the wind.

Ripe fruits are about 25 to 40 mm (1.0 to 1.5 in) long, and solitary or in clusters of two or three; they are subglobose with a yellowish-green, often minutely scurfy, thin husk that is four-winged above the middle. Fruits are slightly flattened. The fruit ripens from September to October and contains bitter-tasting kernels. The drupelike nuts are subglobose, light reddish brown to gray-brown, thin-shelled, two-lobed, and abruptly pointed into a conical head (*10,11,17,21*).

Seed Production and Dissemination—Bitternut hickory seeds are dispersed from September through December. This species does not produce seeds abundantly until the tree is approximately 30 years old. Optimum production extends from 50 to 125 years; trees that are more than 175 years old seldom produce good seed crops (*3*).

Good seed crops occur at 3- to 5-year intervals, with light crops in the intervening years. Bitternut hickory seed is estimated to be from 70 to 85 percent viable (*28*). Germination requires 90 to 120 days. Seeds for all species seldom remain viable when they are in the ground for more than 1 year. Clean bitternut seeds may range from 275 to 410/kg (125 to 185/lb) (*3*).

Seed dissemination is almost entirely by gravity; the fruit is thought to be generally distasteful to wildlife (*35*). Since bitternut grows in wet bottom land, floodwater probably influences its seeding range.

Seedling Development—Embryo dormancy in hickory seed can be overcome by stratification in a moist medium at 0.6° to 4.4° C (33° to 40° F) for 30 to 150 days; when stored for a year or more, seed may require only 30 to 60 days' stratification. Bitternut seeds can probably tolerate a more moist seedbed than most of the other hickories, and it is the least susceptible to frost. Germination is hypogeal. On red clay soil in the Ohio Valley under open or lightly shaded conditions, bitternut hickory seedlings measured 34 cm (13.3 in) in height at 4 years. Sprouts of 1-year-old bitternut seedlings grown on red clay averaged 28 cm (11 in) (*23*).

Vegetative Reproduction—Stump and root sprouting are common among pecan hickories. Bitternut hickory is the most prolific root and stump sprouter of the northern species of hickory, with sprouts arising from stumps, root collar, and roots. Most sprouts from saplings and pole-size trees are at the root collar, and sprouts from sawtimber-size trees are root suckers. Stump sprouts are usually less numerous than root collar sprouts or root suckers (*9,23*). Bitternut hickory develops a dense root system and can be transplanted more successfully than other hickories. For this reason, it may have promise as root stock for grafting and budding; however, propagation is usually by seed, with best results in early spring (*10,13,20*). Techniques for selecting, packing, and storing hickory propagation wood have been described (*19*).

Sapling and Pole Stages to Maturity

Growth and Yield—Bitternut hickory typically attains a height of about 30 m (100 ft) and 61 to 91 cm (24 to 36 in) in d.b.h. The tree attains its best height growth in the rich bottom lands of the lower Ohio River Basin (*7*). Its life span is about 200 years.

Second-growth bitternut hickory on a good site in the Ohio Valley reached the following average heights and diameters (*23*):

	Height		Age d.b.h.	
yr	*m*	*ft*	*cm*	*in*
10	3.0	10	5	2.0
20	7.3	24	10	4.0
30	12.2	40	15	6.0
40	15.8	52	19	7.6
50	18.9	62	23	9.2
60	21.0	69	29	11.4
70	—	—	33	13.0

Growth rates (d.b.h.) of hickory species have been compared to other species in Appalachian hardwood stands as follows (*29*): dominant-codominant hickories 38 to 51 cm (15 to 20 in) in d.b.h. in well-stocked stands on good oak sites grew slower than northern red oak, yellow-poplar, black cherry (*Prunus serotina*), and sugar maple (*Acer saccharum*). Hickories grew about the same as chestnut oak (*Quercus prinus*), white oak, sweet birch (*Betula lenta*), and American beech (*Fagus grandifolia*). Diameter growth for hickory was about 0.3 cm (0.12 in) per year; it was about 0.5 cm (0.20 in) for black cherry and about 0.6 cm (0.23 in) for yellow-poplar and red oak. Equations are available for predicting merchantable gross volumes from hickory stump diameters in Ohio (*12*). Also, procedures are described for predicting diameters and heights and for developing volume tables to any merchantable top diameter for hickory species in southern Illinois and West Virginia (*22,37*).

Bitternut hickory generally prunes itself more readily than other hickories. Epicormic branching is not a problem with hickory species, but occasionally a few branches do occur (*27,29*). In bitternut hickory, the ratio of sapwood to heartwood is low; sapwood seldom is more than 38 mm (1.5 in) wide or more than 25 years old (*23*). Bitternut hickory is the hardiest of the hickories (*26*), as indicated by its wide geographic range.

Rooting Habit—Bitternut hickory develops a dense root system with a pronounced taproot. It is windfirm and can be transplanted more successfully than any other hickory species (*20*).

Early root growth is primarily into the taproot, which typically reaches a depth of 30 to 91 cm (12 to 36 in) during the first year (*32*). Small laterals originate throughout the length of the taproot but may die back during the fall. During the second year, the taproot may reach a depth of 122 cm (48 in) and the laterals grow rapidly. After about 5 years or so, the root system attains its maximum depth, and the horizontal spread of the roots is about double that of the branches. By age 10, the height of the top is about four times the depth of the taproot while the spread of the crown branches is only about half that of the root system.

Mature pecan hickory root systems have a deep taproot, with lateral roots emerging at nearly right angles to the taproot, but no major lateral roots. Pecan hickory roots begin to develop just before spring shoot growth. Roots are more responsive to favorable conditions of soil or climate, and conversely more sensitive to adverse conditions. Depending on environmental conditions, there are usually four to eight cycles of root growth during the year (*32*).

Reaction to Competition—Bitternut hickory is considered intolerant of shade but seems to have a higher seedling tolerance on bottom lands than most of its associates (*24*). Hickories also can be intermediate in tolerance (*23,29*). Bitternut is less susceptible to frost damage than other hickories (*24*).

Silvicultural practices for managing the oak-hickory type are summarized by Watt et al. (*36*). Establishing hickory trees from seedlings is difficult because of seed predators. Infrequent bumper seed crops usually provide some seedlings, but seedling survival is poor under a dense canopy. Because of its prolific sprouting ability, hickory reproduction can survive browsing, breakage, drought, and fire. Top dieback and resprouting may occur frequently, with each successive shoot attaining a larger size and developing a stronger root system than its predecessors (*16*). By this process, hickory reproduction gradually accumulates and develops under moderately dense canopies, especially on sites dry enough to restrict reproduction of more tolerant, but more fire- or drought-sensitive species.

Wherever hickory advance reproduction is adequate, clearcutting results in fast-growing sapling stands of hickories. If there is no advance hickory reproduction, clearcutting eliminates hickories except for stump sprouts. Theory suggests that light thinnings or shelterwood cuts can be used to create advance hickory regeneration, but this has not been demonstrated.

Damaging Agents—Bitternut hickory saplings are easily damaged by fire, and older trees also are susceptible to fire damage because of the low insulating capacity of the hard bark (*13,24*). It is not affected by severe diseases but has many of the problems common to most hickories; these include mineral streaks and sapsucker-induced streaks that degrade lumber. White heart rot *(Poria spiculosa)* is the most widespread and damaging disease of hickory. This trunk rot can produce extensive decay from wounds. A common white wood rot *(Phellinus igniarius)* also attacks bitternut hickory through fire wounds. Occasionally Nectria *(Nectria galligena)* and Strumella *(Strumella coryneoidea)* produce cankers on the stems of bitternut hickory, but most fungi cause little, if any, decay in small young trees. In general, the hard, strong, durable wood of hickories makes them relatively resistant to decay fungi *(2,10,13)*.

Foliage diseases such as leaf mildew, witches' broom *(Microstroma juglandis)*, and leaf blotch *(Mycosphaerella dendroides)* occur on all hickory species. Pecan scab *(Cladosporium effusum)* also occurs on foliage, and bitternut hickory is a host to anthracnose *(Gnomonia caryae)*.

Nuts of all hickory species are susceptible to attack by the hickory nut weevil *(Curculio caryae)*. Another weevil *(Conotrachelus aratus)* attacks young shoots and leaf petioles. The *Curculio* species are the most damaging, often destroying 65 percent of the hickory nut crop *(1)*.

The most important bark beetle attacking bitternut hickory is the hickory bark beetle *(Scolytus quadrispinosus)*. Attacks by this insect are more serious during drought years and where hickory species are growing rapidly. The twig girdler *(Oncideres cingulata)* often seriously deforms trees by severing branches, and sometimes these girdlers even cut hickory seedlings near ground level *(1)*. Two casebearers *(Acrobasis caryivorella* and *A. juglandis)* feed on buds and leaves and later bore into succulent hickory shoots. Larvae of *A. caryivorella* may destroy entire nut sets. The living-hickory borer *(Goes pulcher)* feeds on hickory boles and branches throughout the East. Borers that commonly feed on dying or dead hickories and logs include the banded hickory borer *(Knulliana cincta)*, a long-horned beetle *(Saperda discoidea)*, apple twig borer *(Amphicerus bicaudatus)*, the flatheaded ambrosia beetle *(Platypus compositus)*, redheaded ash borer *(Neoclytus acuminatus)*, and a false powderpost beetle *(Scobicia bidentata)*.

Insects that severely damage lumber and manufactured hickory products include the powderpost beetles *(Lyctus* spp.) and *Polycanon stoutii*. Gall insects *(Caryomyia* spp.) commonly infest leaves. The fruittree leafroller *(Archips argyrospila)* and the hickory leafroller *(Argyrotaenia juglandana)* are the most common leaf feeders. Gypsy moth *(Lymantria dispar)* larvae feed on hickory leaves, but hickories are not the gypsy moth's favorite food. The giant bark aphid *(Longistigma caryae)* is common on the bark of hickories. This aphid feeds on twigs and can cause branch mortality. European fruit lecanium *(Parthenolecanium corni)* is common in hickories *(1)*.

Some birds and mammals eat the nuts when there are less favored hickory nuts available. Together with losses from insects and disease, these virtually eliminate the annual nut production except during bumper seed crop years.

Special Uses

Bitternut is used for lumber and pulpwood. Pecan hickories, such as bitternut, are not equal to true hickories in strength, hardness, and toughness. Based on ovendry weight and green volume, the specific gravity of green bitternut wood is 0.60; at 12 percent moisture content, the specific gravity is 0.66 *(31)*.

Hickory species are most desirable for charcoal and fuelwood; pecan hickories are less desirable than the true hickories. Bitternut hickory ranks third in heating value among hickories *(25)*; it burns with an intense flame and leaves little ash.

Because bitternut hickory wood is hard and durable, it is used for furniture, paneling, dowels, tool handles, and ladders. It is a choice fuel for smoking meats *(15)*. Other uses include bars, crates, pallets, and flooring *(10)*.

Bitternut hickory seeds are eaten by wildlife but are of little value for human consumption because of their high tannin content, and extreme bitterness and astringency *(7,18,26,35)*. Seeds do not usually constitute a large portion of the diet of squirrels. Rabbits, beavers, and small rodents and mammals occasionally feed on the bark of hickory species *(5,35)*. The foliage of bitternut hickory has a high calcium content and is near the top of the list of soil-improving species *(4)*.

Early settlers used oil extracted from the nuts for oil lamps. They also believed the oil was valuable as a cure for rheumatism *(19)*. Bitternut hickory is desirable as an ornamental or shade tree, and the dense root system provides good soil stability.

Genetics

To date, no information has been published concerning population or other genetic studies of this species.

Hickories are well-known for their variability and many natural hybrids among North American species are known. Usually the species within each genus can be successfully intercrossed *(14)*. Bitternut hickory naturally hybridizes with the following species: *C. illinoensis* (*C.* × *brownii* Sarg.), *C. glabra* (*C.* × *demareei* Palmer), and *C. ovata* (*C.* × *laneyi* Sarg.).

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Carya glabra (Mill.) Sweet **Pignut Hickory**

Juglandaceae **Walnut family**

Glendon W. Smalley

Pignut hickory *(Carya glabra)* is a common but not abundant species in the oak–hickory forest association in Eastern United States. Other common names are pignut, sweet pignut, coast pignut hickory, smoothbark hickory, swamp hickory, and broom hickory. The pear-shaped nut ripens in September and October and is an important part of the diet of many wild animals. The wood is used for a variety of products, including fuel for home heating.

Habitat

Native Range

The range of pignut hickory (fig. 1) covers nearly all of eastern United States *(11)*. It extends from Massachusetts and the southwest corner of New Hampshire westward through southern Vermont and extreme southern Ontario to central Lower Michigan and Illinois; southward through extreme southeastern Iowa, Missouri, and Arkansas to Louisiana and parts of East Texas. The species grows eastward through Louisiana and along the Gulf Coast to Mississippi and Alabama into central Florida.

Best development of this species is in the lower Ohio River Basin. It is the hickory most commonly found in the Appalachian forests. Pignut makes up much of the hickory harvested in Kentucky, West Virginia, the Cumberland Mountains of Tennessee, and the hill country of the Ohio Valley.

Climate

Pignut hickory grows in a humid climate with an average annual precipitation of 760 to 2030 mm (30 to 80 in) of which 510 to 1020 mm (20 to 40 in) is rain during the growing season. Average snowfall varies from little to none in the South to 2540 mm (100 in) or more in the mountains of West Virginia, southeastern New York, and southern Vermont *(25)*.

Within the range of pignut hickory, average annual temperatures vary from 7° C (45° F) in the north to 21° C (70° F) in Florida. Average January temperature varies from -4° to 16° C (25° to 60° F) and average July temperature varies from 21° to 27° C (70° to 80° F). Extremes of 46° and -30° C (115° and -22° F) have been recorded within the range. The growing season varies by latitude and elevation from 140 to 300 days.

Mean annual relative humidity ranges from 70 to 80 percent with small monthly differences; daytime relative humidity often falls below 50 percent while nighttime humidity approaches 100 percent.

Mean annual hours of sunshine range from 2,200 to 3,000. Average January sunshine varies from 100 to 200 hours, and July sunshine from 260 to 300 hours. Mean daily solar radiation ranges from 12.57 to 18.86 million J m± (300 to 450 langleys). In January daily radiation varies from 6.28 to 12.57 million J m± (150 to 300 langleys), and in July from 20.95 to 23.04 million J m± (500 to 550 langleys).

According to one classification of climate *(20)*, the range of pignut hickory south of the Ohio River, except for a small area in Florida, is designated as humid, mesothermal. That part of the range lying north of the Ohio River is designated humid, microthermal. Part of the species range in peninsular Florida is classed as subhumid, mesothermal. Mountains in Pennsylvania, West Virginia, North Carolina, and Tennessee are classed as wet, microthermal, and mountains in South Carolina and Georgia are classed as wet, mesothermal. Throughout its range, precipitation is rated adequate during all seasons.

Soils and Topography

Pignut hickory frequently grows on dry ridgetops and sideslopes throughout its range but it is also common on moist sites, particularly in the mountains and Piedmont. In the Great Smoky Mountains pignut hickory has been observed on dry sandy soils at low elevations. Whittaker *(27)* placed pignut in a submesic class and charted it as ranging up to 1480 m (4,850 ft)—the hickory with the greatest elevational range in the Great Smoky Mountains. In southwest Virginia, south-facing upper slopes from 975 to 1050 m (3,200 to 3,445 ft) of Beanfield Mountain are dominated by pignut hickory, northern red oak *(Quercus rubra)*, and white oak *(Q. alba)*. This site is the most xeric habitat on the mountain because of high insolation, 70 percent slopes, and medium- to coarse-textured soils derived from Clinch sandstone. Mid-elevation slopes from 800 to 975 m (2,625 to 3,200 ft) are dominated by chestnut oak *(Q. prinus)*, northern red oak, and pignut hickory and coincide with three shale formations *(12)*.

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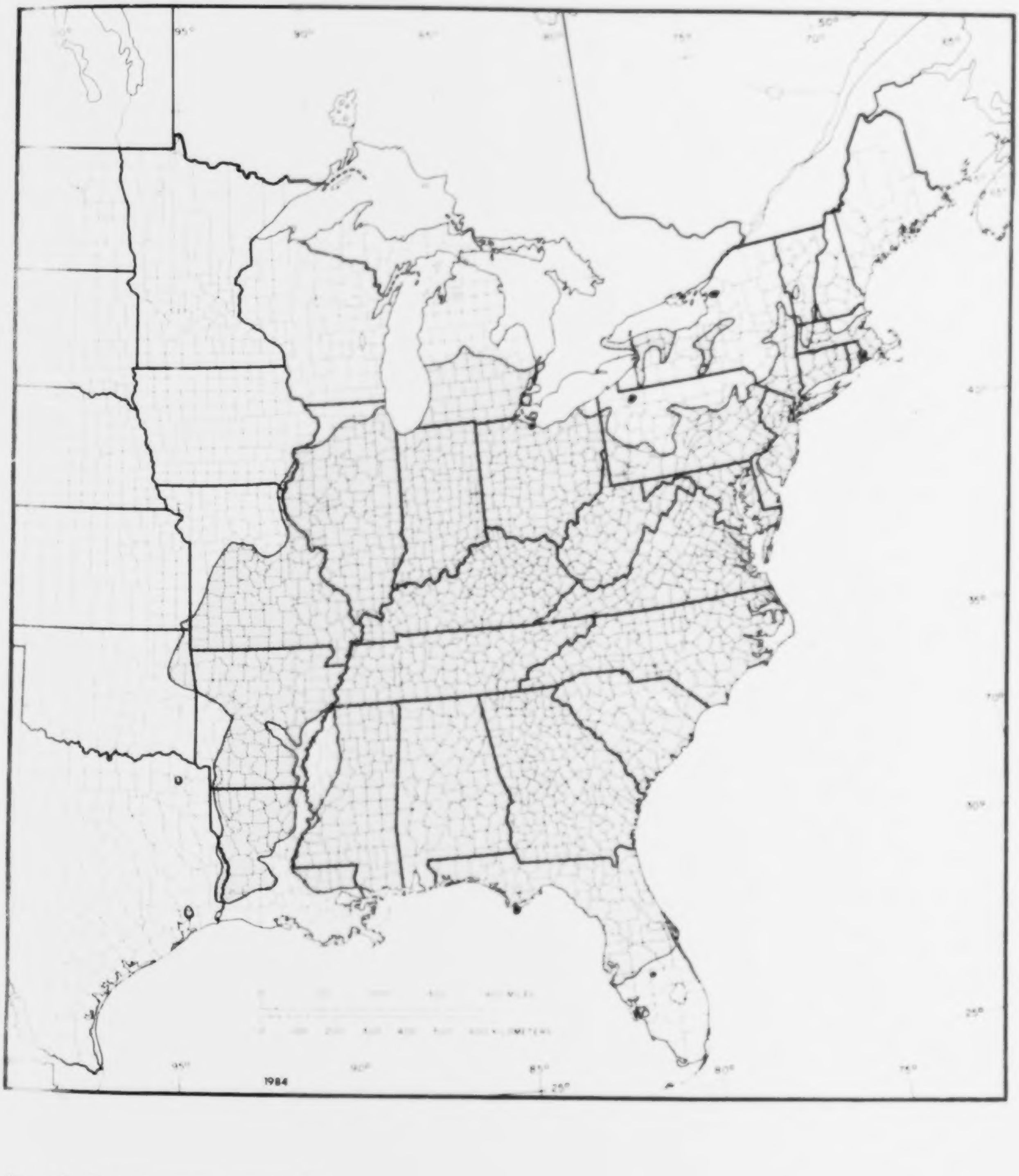
95°
90°
85°
80°
75°
70°
65°
50°
40°
35°
30°
25°
1984

Figure 1—*The native range of pignut hickory.*

The range of pignut hickory encompasses 7 orders, 12 suborders, and 22 great groups of soils *(24,25)*. About two-thirds of the species range is dominated by Ultisols, which are low in bases and have subsurface horizons of clay accumulation. They are usually moist but are dry during part of the warm season. Udults is the dominant suborder and Hapludults and Paleudults are the dominant great groups. These soils are derived from a variety of parent materials—sedimentary and metamorphic rocks, glacial till, and in places varying thickness of loess—which vary in age from Precambrian to Quaternary.

A wide range of soil fertility exists as evidenced by soil orders—Alfisols and Mollisols which are medium to high in base saturation to Ultisols which are low in base saturation *(24)*. Pignut hickory responds to increases in soil nitrogen similarly to American beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum)*, and blackgum *(Nyssa sylvatica) (15)*. These species are rated as intermediate in nitrogen deficiency tolerance and consequently are able to grow with lower levels of nitrogen than are required by "nitrogen-demanding" white ash *(Fraxinus americana)*, yellow-poplar *(Liriodendron tulipifera)*, and American basswood *(Tilia americana)*. Hickories are considered "soil improvers" because their leaves have a relatively high calcium content.

Associated Forest Cover

Hickories are consistently present in the broad eastern upland climax forest association commonly called oak–hickory, but they are not generally abundant *(18)*. Locally, hickories may make up to 20 to 30 percent of stand basal area, particularly in slope and cove forests below the escarpment of the Cumberland Plateau *(23)* and in second-growth forests in the Cumberland Mountains, especially on benches *(14)*. It has been hypothesized that hickory will replace chestnut *(Castanea dentata)* killed by the blight *(Cryphonectria parasitica)* in the Appalachian Highlands *(10,12)*. On Beanfield Mountain in Giles County, VA, the former chestnut–oak complex has changed to an oak–hickory association over a period of 50 years. This association is dominated by pignut hickory with an importance value of 41.0 (maximum value = 300), northern red oak (36.0), and chestnut oak (25.0). White oak, red maple *(Acer rubrum)*, and sugar maple are subdominant species.

Pignut hickory is an associated species in 20 of the 90 forest cover types listed by the Society of American Foresters for the eastern United States *(6)*:

Northern Forest Region

53	White Pine–Chestnut Oak

Central Forest Region

40	Post Oak–Blackjack Oak
44	Chestnut Oak
45	Pitch Pine
46	Eastern Redcedar
52	White Oak–Black Oak–Northern Red Oak
53	White Oak
55	Northern Red Oak
57	Yellow-Poplar
59	Yellow-Poplar–White Oak–Northern Red Oak
64	Sassafras–Persimmon
110	Black Oak

Southern Forest Region

75	Shortleaf Pine
76	Shortleaf Pine–Oak
78	Virginia Pine–Oak
79	Virginia Pine
80	Loblolly Pine–Shortleaf Pine
81	Loblolly Pine
82	Loblolly Pine–Hardwood
83	Longleaf Pine–Slash Pine

Because the range of pignut hickory is so extensive, it is not feasible to list the associated trees, shrubs, herbs, and grasses, which vary according to elevation, topographic conditions, edaphic features, and geographic locality.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Hickories are monoecious and flower in the spring *(3)*. The staminate catkins of pignut hickory are 8 to 18 cm (3 to 7 in) long and develop from axils of leaves of the previous season or from inner scales of the terminal buds at the base of the current growth. The pistillate flowers appear in spikes about 6 mm (0.25 in) long on peduncles terminating in shoots of the current year. Flowers open from the middle of March in the southeast part of the range to early June in New England. The catkins usually emerge before the pistillate flowers.

The fruit of hickory is pear shaped and enclosed in a thin husk developed from the floral involucre. The fruit ripens in September and October, and seeds are dispersed from September through December. Husks are green until maturity; they turn brown to brownish-black as they ripen. The husks become dry at maturity and split away from the nut into four valves along sutures. Husks of pignut hickory split only to the middle or slightly beyond and generally cling to the nut, which is unribbed, with a thick shell.

Seed Production and Dissemination—Pignut hickory begins to bear seed in quantity in 30 years, with optimum production between 75 and 200 years *(16)*. The maximum age for seed production is about 300 years. Good seed crops occur every year or two with light crops in other years; frost can seriously hinder seed production *(22)*. Usually less than half of the seeds are sound *(2,3)*, but 50 to 75 percent of these will germinate. The hickory shuckworm (*Laspeyresia caryana*) can seriously reduce germination. Pignut seed, averaging 440/kg (200/lb), is lighter than the seed of other hickory species. The nuts are disseminated mainly by gravity, but the range of seeding is extended by squirrels and chipmunks.

Seedling Development—Hickories exhibit embryo dormancy which is overcome naturally by overwintering in the duff and litter or artificially by stratification in a moist medium at 1° to 4° C (33° to 40° F) for 30 to 150 days. In forest tree nurseries unstratified hickory nuts are sown in the fall and stratified nuts are sown in the spring. Hickories are hypogeously germinating plants, and the nuts seldom remain viable in the forest floor for more than one winter *(22)*.

Seedling growth of hickories is slow. The following height growth of pignut hickory seedlings was reported in the Ohio Valley in the open or under light shade, on red clay soil *(2)*:

Age	Height	
yr	*cm*	*in*
1	8	3.0
2	15	5.8
3	20	8.0
4	30	12.0
5	43	17.0

Vegetative Reproduction—Hickories sprout readily from stumps and roots. Stump sprouting is not as prolific as in other deciduous trees species but the sprouts that are produced are vigorous and grow fairly rapidly in height. Root sprouts also are vigorous and probably more numerous than stump sprouts in cut-over areas. Small stumps sprout more frequently than large ones. Sprouts that originate at or below ground level and from small stumps are less likely to develop heartwood decay. Pignut hickory is difficult to reproduce from cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—Pignut hickory often grows 24 to 27 m (80 to 90 ft) tall and occasionally reaches 37 m (120 ft), with d.b.h. of 91 to 122 cm (36 to 48 in) (fig. 2). The bole is often forked. Height and diameter by age are shown in table 1 for selected locations. Diameter growth of pignut hickory (along with chestnut oak, white oak, sweet birch (*Betula lenta*), and American beech is rated slow. Since hickories constitute 15 percent or less of the basal area of oak-hickory forest types, most growth and yield information is written in terms of oak rather than oak-hickory. Yields of mixed oak stands *(5,7,19)* and of hickory stands *(2)* have been reported. Tree volume tables are available *(2,19)*.

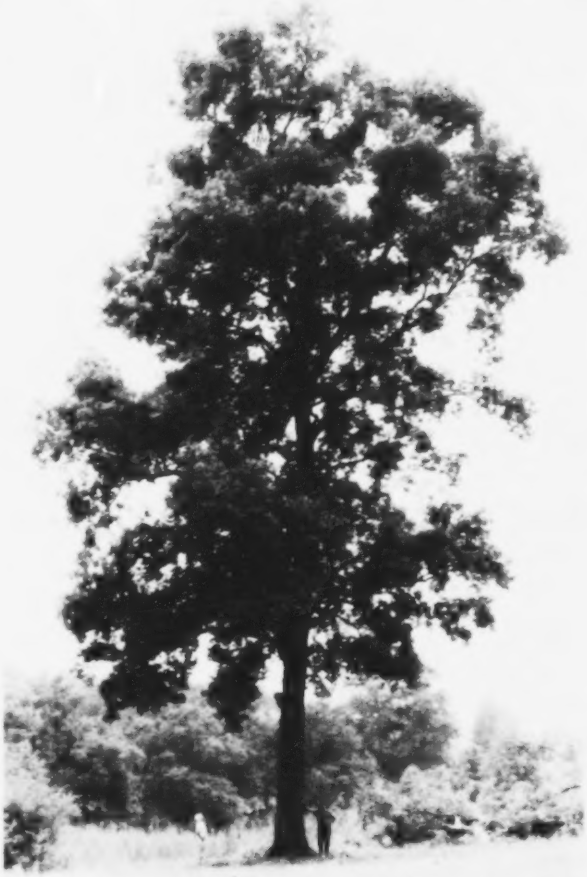

Figure 2—*A mature pignut hickory about 27 m (90 ft) tall.*

Rooting Habit—Pignut hickory tends to develop a pronounced taproot with few laterals and is rated as windfirm *(21)*. The taproot develops early, which may explain the slow growth of seedling shoots. Taproots may develop in compact and stony soils.

Table 1—Diameter and height of pignut hickory in selected geographic areas (adapted from *2*)

	D.b.h.	Height			
Age	S. Indiana and N. Kentucky[1]	Ohio Valley[1]	Northern Ohio[1]	Cumberland Mountains[2]	Mississippi Valley[2]
yr	*cm*	*m*			
10	2	2.7	2.1	1.8	1.8
20	5	5.8	6.1	4.3	5.8
30	8	9.8	10.7	7.3	8.2
40	11	12.8	14.6	9.8	10.4
50	14	15.5	18.6	12.2	12.2
60	17	17.7	21.0	14.6	14.0
70	21	19.5	22.6	16.8	15.8
80	25	21.0	—	18.9	17.7
yr	*in*	*ft*			
10	1.0	9	7	6	6
20	2.0	19	20	14	19
30	3.2	32	35	24	27
40	4.4	42	48	32	34
50	5.5	51	61	40	40
60	6.8	58	69	48	46
70	8.4	64	74	55	52
80	10.0	69	—	62	58

[1] Second growth
[2] Virgin forest

Reaction to Competition—The hickories as a group are classed as intermediate in shade tolerance; however, pignut hickory has been classed as intolerant in the Northeast and tolerant in the Southeast. In much of the area covered by mixed oak forests, shade-tolerant hardwoods (including the hickories) are climax, and the trend of succession toward this climax is very strong. Although most silvicultural systems when applied to oak types will maintain a hardwood forest, the cutting methods used affects the rapidity with which other species may replace the oaks and hickories *(17,18,26)*.

Damaging Agents—Pignut hickory is easily damaged by fire, which causes stem degrade or loss of volume, or both. Internal discolorations called mineral streak are common and are one major reason why so few standing hickories meet trade specifications. Streaks result from yellow-bellied sapsucker pecking, pin knots, worm holes, and mechanical injuries. Hickories strongly resist ice damage and seldom develop epicormic branches.

The Index of Plant Diseases in the United States lists 133 fungi and 10 other causes of diseases on *Carya* species *(4,9)*. Most of the fungi are saprophytes, but a few are damaging to foliage, produce cankers, or cause trunk or root rots.

The most common disease of pignut hickory from Pennsylvania southward is a trunk rot caused by *Poria spiculosa*. Cankers vary in size and appearance depending on their age. A common form develops around a branch wound and resembles a swollen, nearly healed wound. On large trees these may become prominent burl-like bodies having several vertical or irregular folds in the callus covering. A single trunk canker near the base is a sign that the butt log is badly infected, and multiple cankers are evidence that the entire tree may be a cull.

Major leaf diseases are anthracnose *(Gnomonia caryae)* and mildew *(Microstroma juglandis)*. The former causes brown spots with definite margins on the undersides of the leaf. These may coalesce and cause widespread blotching. Mildew invades the leaves and twigs and may form witches' brooms by stimulating bud formation. Although locally prevalent, mildew offers no problem in the management of hickory.

The stem canker *(Nectria galligena)* produces depressed areas with concentric bark rings that develop on the trunk and branches. Affected trees are sometimes eliminated through breakage or competition and sometimes live to reach merchantable size with cull section at the canker. No special control measures are required, but cankered trees should be harvested in stand improvement operations.

A gall-forming fungus species of *Phomopsis* can produce warty excrescences ranging from small twig galls to very large trunk burls on northern hickories and oaks. Little information is available on root diseases of hickory.

More than 100 insects have been reported to infest hickory trees and wood products, but only a few cause death or severe damage *(1)*. The hickory bark beetle *(Scolytus quadrispinosus)* is the most important insect enemy of hickory, and also one of the most important insect pests of hardwoods in the Eastern United States. During drought periods in the Southeast, outbreaks often develop and large tracts of timber are killed. At other times, damage may be confined to the killing of a single tree or to portions of the tops of trees. The foliage of heavily infested trees turns red within a few weeks after attack, and the trees soon die. There is one generation per year in northern areas and normally two broods per year in the South. Control consists of felling infested trees and destroying the bark during winter months or storing infested logs in ponds.

Logs and dying trees of several hardwood species including pignut hickory are attacked by the ambrosia beetle *(Platypus quadridentatus)* throughout the South and north to West Virginia and North Carolina. The false powderpost beetle *(Xylobiops basilaris)* attacks recently felled or dying trees, logs, or limbs with bark in the Eastern and

Southern States. Hickory, persimmon (*Diospyros virginiana*), and pecan (*C. illinoensis*) are most frequently infested, but other hardwoods also are attacked. Healthy trees growing in proximity to heavily infested trees are occasionally attacked but almost always without success. Hickory and persimmon wood (useful in the manufacture of small products such as shuttle blocks, mallets, and mauls) is sometimes seriously damaged.

Hickory is one of several host species of the twig girdler (*Oncideres cingulata*). Infested trees and seedlings are not only damaged severely but become ragged and unattractive. A few of the more common species of gall-producing insects attacking hickory are *Phylloxera caryaecaulis*, *Caryomyia holotricha*, *C. sanguinolenta*, and *C. tubicola*.

Special Uses

Hickories provide food to many kinds of wildlife *(8, 13)*. The nuts are relished by several species of squirrel and represent an estimated 10 to 25 percent of their diet. Nuts and flowers are eaten by the wild turkey and several species of songbirds. Nuts and bark are eaten by black bears, foxes, rabbits, and raccoons. Small mammals eat the nuts and leaves; 5 to 10 percent of the diet of eastern chipmunks is hickory nuts. White-tailed deer occasionally browse hickory leaves, twigs, and nuts.

The kernel of hickory seeds is exceptionally high in crude fat, up to 70 to 80 percent in some species. Crude protein, phosphorus, and calcium contents are generally moderate to low. Crude fiber is very low.

Pignut hickory makes up a small percentage of the biomass in low-quality upland hardwood stands that are prime candidates for clearcutting for chips or fuelwood as the first step toward rehabilitation to more productive stands. Hickory has a relatively high heating value and is used extensively as a home heating fuel.

Pignut hickory is an important shade tree in wooded suburban areas over most of the range but is seldom planted as an ornamental tree.

Genetics

Carya glabra var. *megacarpa* (Sarg.) Sarg., coast pignut hickory, was once recognized as a distinct variety but is now considered to be a synonym of *C. glabra* (Mill.) Sweet. *C. leiodermis* Sarg., swamp hickory, has also been added as a synonym of *C. glabra* *(11)*.

Carya glabra (Mill.) Sweet var. *glabra* distinguishes the (typical) pignut hickory from red hickory (*C. glabra* var. *odorata* (Marsh.) Little). The taxonomic position of red hickory is controversial. The binomial *C. ovalis* (Wangenh.) Sarg. was published in 1913 for a segregate of *C. glabra*. It was reduced to a synonym of *C. glabra* in Little's 1953 checklist but was elevated to a variety in the 1979 edition *(11)*. The principal difference is in the husk of the fruit, opening late and only partly, or remaining closed in *C. glabra* but promptly splitting to the base in *C. ovalis*. However, many trees are intermediate in this trait, and the recorded ranges are almost the same. The leaves of *C. ovalis* have mostly seven leaflets; those of *C. glabra* have mostly five leaflets. The two can be distinguished with certainty only in November. Since the two ranges seem to overlap, the distributions have been mapped together as a *Carya glabra-ovalis* complex *(11)*.

Carya ovalis has also been treated as an interspecific hybrid between *C. glabra* and *C. ovata*. *C. ovalis* was accepted as a polymorphic species especially variable in the size and shape of its nuts and possibly a hybrid. The relationships may be more complex after a long and reticulate phylogeny, according to detailed chemical analyses of hickory nut oils.

One hybrid, *C. × demareei* Palmer (*C. glabra × cordiformis*) was described in 1937 from northeastern Arkansas.

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Carya illinoensis (Wangenh.) K. Koch   Pecan

Juglandaceae   Walnut family

J. K. Peterson

Pecan (*Carya illinoensis*) is one of the better-known pecan hickories. It is also called sweet pecan and in its range where Spanish is spoken, nogal morado or nuez encarcelada. The early settiers who came to America found pecans growing over wide areas. These native pecans were and continue to be highly valued as sources of new varieties and as stock for selected clones. Besides the commercial edible nut that it produces, the pecan provides food for wildlife. Pecans are an excellent multipurpose tree for the home landscape by providing a source of nuts, furniture-grade wood, and esthetic value.

Habitat

Native Range

Pecan (fig. 1) grows principally in the lower Mississippi Valley. Within this region it extends westward to eastern Kansas and central Texas.

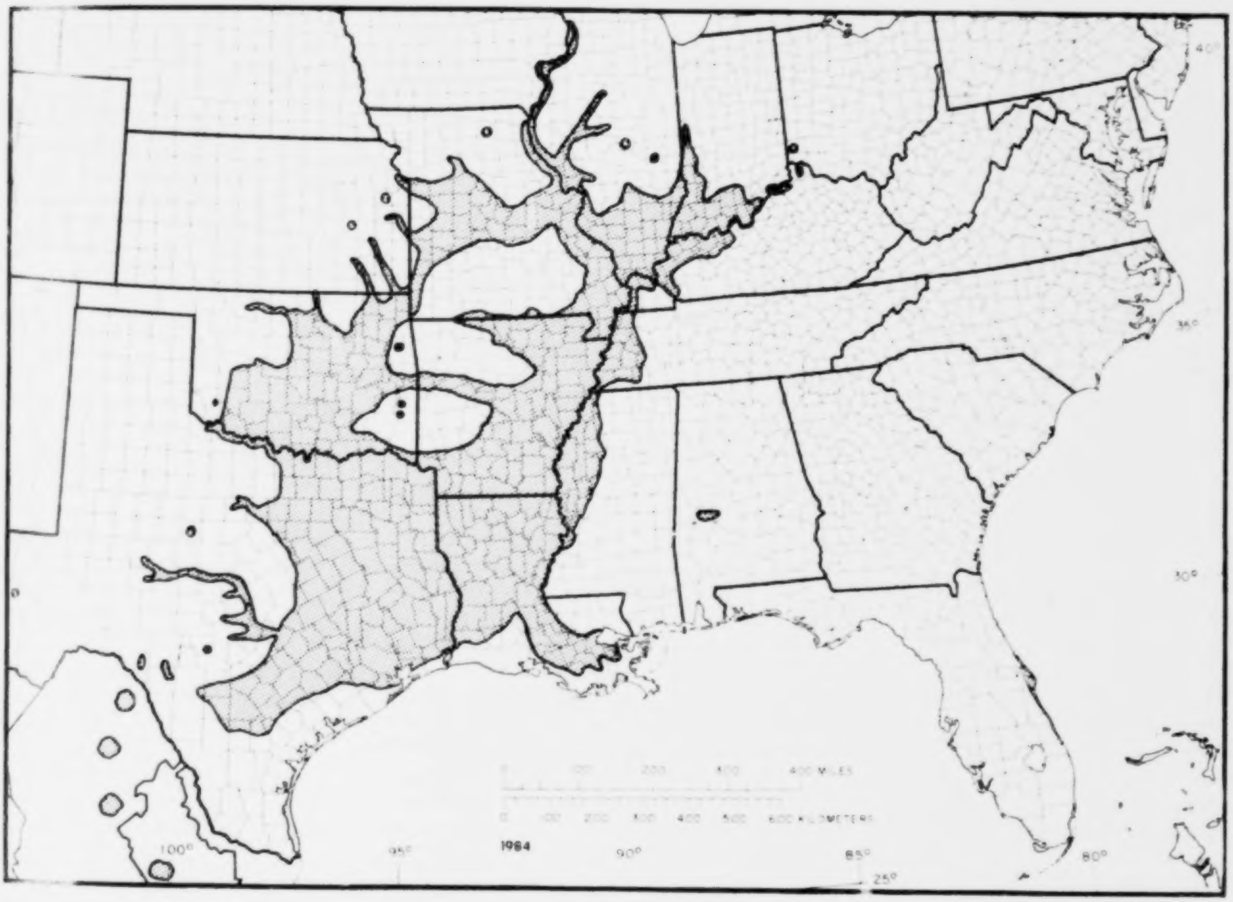

Figure 1—*The native range of pecan.*

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eastward to western Mississippi and western Tennessee. Sparse occurrence has been reported along the eastern margin of its range from southwestern Ohio to Kentucky and Alabama. Pecan also grows locally throughout northeastern and central Mexico *(34)*.

Climate

Pecan grows in a humid climate; the minimum average annual rainfall approximates 760 mm (30 in) and the maximum reaches 2010 mm (79 in). At least 510 mm (20 in) of rain falls during the growing season. Annual snowfall varies from 0 to 50 cm (0 to 20 in). Mean summer temperatures range as high as 27° C (81° F), with extremes of 41° to 46° C (105° to 115° F). Average winter temperatures vary from 10° to -1° C (50° to 30° F), with extremes of -18° to -29° C (0° to -20° F) *(2,26,27)*.

Soils and Topography

Sweet pecan grows commonly on well-drained loam soils which are not subject to prolonged flooding. However, it does appear on heavy textured soils, where it is limited to alluvial soils of recent origin. On such land forms its best development is on the ridges and well-drained flats. It rarely grows on low and poorly drained clay flats where it is replaced by water hickory *(Carya aquatica) (2,21)*. These soils are most commonly found in the orders Entisols, Inceptisols, and Alfisols. Pecan seedlings can survive short periods of flooding *(18)*.

Associated Forest Cover

Pecan is a major component of the Society of American Foresters forest cover type: Sycamore-Sweetgum-American Elm (Type 94) but is more prominent in a variant of this type: the Sycamore-Pecan-American Elm association. In addition, it is a component of Cottonwood (Type 63) and Black Willow (Type 95) *(32)*. Other associated species are green ash *(Fraxinus pennsylvanica)*, sugarberry or hackberry *(Celtis* spp.), boxelder *(Acer negundo)*, silver maple *(A. saccharinum)*, and water oak *(Quercus nigra)*. Some common understory components include pawpaw *(Asimina triloba)*, giant cane *(Arundinaria gigantea)*, and pokeweed *(Phytolacca americana)*. Vines often present are poison-ivy *(Toxicodendron radicans)*, grape *(Vitis* spp.), Alabama supplejack *(Berchemia scandens)*, greenbriers *(Smilax* spp.), and Japanese honeysuckle *(Lonicera japonica)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowering of pecan takes place from April through May. The species is monoecious; flowers are borne in staminate and pistillate catkins on the same tree. Staminate flowers appear in slender fascicled, sessile catkins, 8 to 15 cm (3 to 6 in) long. The calix is two- or three-lobed, with a center lobe that is longer than the lateral ones, and five or six stamens. Pistillate catkins are hairy, yellow, and not as numerous as staminate ones, with two to four stigmas *(37)*. Most pecan cultivars are clones derived from wild trees. These cultivars generally show incomplete dichogamy. In some cultivars there is no overlap at all in the period of pollen dehiscence and stigma receptivity, thus requiring more than one cultivar for successful pollination and fruit set *(20)*. Pecan is anemophilous, and excessive rainfall during the flowering period may prevent pollination.

Beginning in late summer, buds of pecan develop a physiological state of rest, characterized by loss of apical dominance and cessation of both terminal and lateral growth. Existence of a cold requirement was first indicated by Waite *(38)*. Intensity and dissipation of rest depend on the temperature regimes and genetic factors *(4)*.

Seed Production and Dissemination—Fruits ripen in September and October and are dispersed from September through December *(8)*. Pecan fruits are ovoid, globose or pear-shaped nuts, enclosed in husks developed from the floral involucre. The green husks turn brown to black as they ripen. The husks become dry at maturity and split away from the nut in four valves along sutures starting from the base. The minimum seed-bearing age is 2 to 4 years in some cultivars and up to 20 years for individuals in natural stands. The maximum seed-bearing age also varies considerably; a maximum of 300 years has been reported *(37)*. The cleaned nuts average about 220 to 350/kg (100 to 160/lb). Good crops are produced at intervals from 1 to 3 years. Seed dispersal is principally by water and animals. The floating nuts can be carried considerable distances by flood water. Aerial dispersion is mainly by squirrels *(21)*.

Seedling Development—Seeds can be stored for 3 to 5 years in closed containers at 5° C (41° F) and 90 percent relative humidity *(8)*. Seed stratification and germination conditions have been reported by various authors *(3,6,12,36)*. As with all hickories, germination is hypogeal. Seeds of pecan show delayed germination, since the shell mechanically restricts radicle elongation. To overcome this delay the nuts are stratified at 2° to 5° C (36° to 41° F) for 30 to 90 days, followed by incubation at room temperature. However, the restriction can be nullified by incubating the nuts at 30° to 35° C (86° to 95° F), without prior stratification. Under this regime, uniform and rapid germination occurs and is completed in 20 days. Germination without prior stratification is greatly enhanced by soaking the nuts in gibberellic acid (*7*).

Under natural conditions, pecan nuts remain dormant until spring when germination starts in early April and extends to early June. Exceptionally dry weather or heavy aerial competition greatly reduces survival. On loamy soils height growth averages about 90 cm (35 in) per year for several years under favorable weather conditions (*21*).

Vegetative Reproduction—Rooting experiments with shoot cuttings gave highly variable success rates. The principal variables were time of collection, thickness and origin of cuttings, chemical treatments, and genetic factors. Softwood cuttings are easier to root than hardwood or semi-hardwood cuttings. The time of shoot collection, however, seems most important. Juvenile cuttings, taken about midway of the dormant season and dipped in 10,000 p/m indolebutyric acid, gave 100 percent rooting; adult wood rooted 85 percent under these conditions (*31*). Shoots derived from adventitious buds root better than other shoots, especially when terminal buds are removed (*14*). The optimum collection period for pecan cuttings appears to be during mid-rest or after 200 to 400 hours of field chilling below 72° C (45° F) have accumulated. Cuttings collected after 500 hours chilling force buds rather than roots (*19*). Softwood cuttings may root in 15 days and flush after 35 days (*30*). Air-layering is also successful in pecans; the timing of this treatment is very essential (*25*). Pecan can also be regenerated from the stump. If the strongest shoot is trained as the new tree, while the others are removed, vigorous growth will result (*40*). Commercial cultivars may be propagated by grafting on improved root stocks.

Sapling and Pole Stages to Maturity

Growth and Yield—On loamy soils, height growth may average 90 cm (35 in) per year for several years (*21*). Diameter growth of pecan parallels the average for bottom lands. The average 10-year diameter growth in natural unmanaged stands in the northeast Louisiana delta is 5 cm (2.0 in) in the 15 to 30 cm (6 to 12 in) diameter class, 7 cm (2.7 in) in the 35 to 45 cm (14 to 18 in) diameter class, 5 cm (2 in) in the 50 to 70 cm (20 to 28 in) diameter class, and 6 cm (2.3 in) in the 75 cm (30 in) diameter class (*5*).

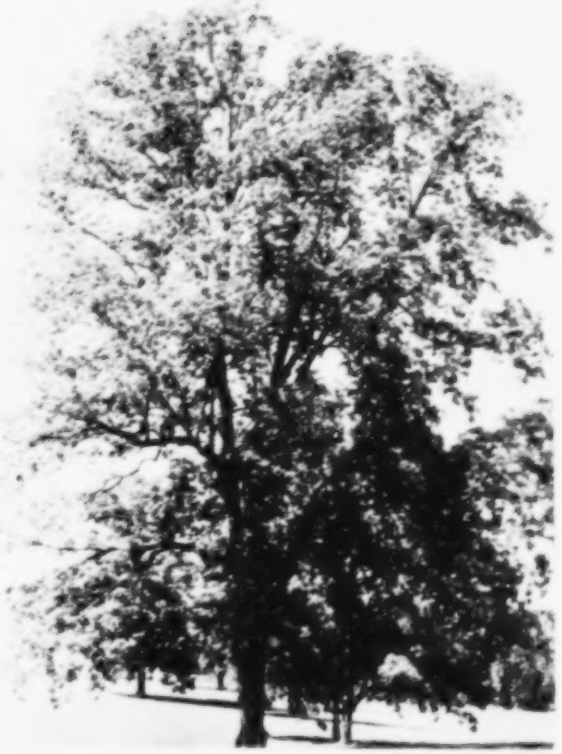

Figure 2—*An open-grown pecan.*

Mature pecan is a medium to very large straight-stemmed tree reaching up to 55 m (180 ft) in height and occasionally 180 to 210 cm (70 to 83 in) in d.b.h. (*21*) (fig. 2).

Rooting Habit—No information available.

Reaction to Competition—Pecan is classed as intolerant of shade but more tolerant than cottonwood and willow. It is a subclimax species. Pecan responds well to release in all age groups, provided that the trees have good vigor (*21*).

Damaging Agents—Only the most common fungal diseases are listed here. A spot anthracnose, *Elsinoe randii*, causes an important nursery blight. Small reddish lesions form on both leaf surfaces. Tissue falls out of the spots, producing holes and ragged leaf margins (39). *Cladosporium effusum* (pecan scab) is a limiting factor in nut production in parts of the South. Lesions along the veins and underside of the leaves are produced (15). *Gnomonia nervisedа* (vein spot), *G. caryae*, and *G. caryae* var. *pecanae* (liver spot) are common (34). *Microstroma juglandis* causes leafspot or white mold as well as witches' brooms. *Cercospora halstedii*, the conidial stage of *Mycosphaerella dendroides* (9), causes leaf blotch. *Mycosphaerella caryigena*, known as downy spot, causes frosty spots on the lower leaf surfaces (23).

A large number of fungi rot the woody cylinder of living hickories. Some rot heartwood; others rot senescent or dead sapwood. Prominent genera are *Fomes*, *Poria*, and *Polyporus* (15). *Poria spiculosa* is a most damaging and common canker that produces thick, deep callus folds. It appears as rough circular swellings on the bole (33). *Phomopsis* tumor is a widespread gall-forming fungus. It produces from warty growths on twigs to large burls on trunks (34).

Among the common root rot diseases are *Clitocybe tabescens*, *Phymatotrichum omnivorum* (Texas root rot), and *Helicobasidium purpureum* (violet root rot). Feeder root necrosis is produced by *Fusarium solani*, *F. oxysporum*, and *Pythium irregulare*.

Other diseases include *Criconemoides quadricornis*, a "ring" nematode (16), and *Agrobacterium tumefaciens*, an economically important bacterial disease in pecan. In the South pecan is affected by a viral brooming disorder that results in a dense growth of willowy shoots (22). Pecan rosette is a common bunching disease in the South caused by zinc deficiency (10).

Many insects feed on pecan leaves, nuts, twigs, wood, and roots (11,24). Among the beetles are *Goes pulcher*, the living hickory borer, whose larvae feed on trunks and branches; they are common throughout the United States. *Oncideres cingulata*, twig girdler, and *O. pustulatus*, hinsache girdler, are wood borers that at times become numerous. Adult females girdle branches, which then die and fall off. Occasionally young seedlings may be cut off near the ground. The hickory bark beetle (*Scolytus quadrispinosus*) bores into boles and branches and can do considerable damage. Severe outbreaks causing extensive tree mortality occur when precipitation is insufficient in summer. The flat oak borer (*Smodicum cucujiforme*) attacks heartwood of trees as well as cut lumber. This beetle occurs throughout the Eastern United States. The so-called pinhole borers (*Xyleborus affinis*, *X. ferrugineus*, and *Xyleborinus saxesensi*) inhabit trunks and stems of many hardwoods, including pecan, in the Southeastern United States. They primarily attack trees weakened by drought, mechanical damage, or cold injury. Occasionally they attack healthy trees but rarely cause serious damage since the larvae cannot subsist on wood with good sap flow. The hickory shoot curculio (*Conotrachelus aratus*) feeds on unfolding buds and young shoots of pecan and may cause extensive damage. The nut curculio (*Conotrachelus hicoriae*) attacks immature pecan nuts. Both beetle species occur in the Pecan Belt. The flatfooted ambrosia beetle (*Platypus compositus*) causes injuries in freshly felled trees due to extensive burrowing. This beetle occurs throughout the Southern United States. The tilehorned root borer (*Prionus imbricornis*) and the broadnecked root borer (*Prionus laticollis*) are beetles whose larvae feed on root bark of living trees. They soon enter the roots, completely hollowing and occasionally severing them.

Other injurious insects include the following: the sycamore lacebug (*Corythucha ciliata*), which feeds on leaves of pecan, and is common in the Eastern United States (13); the forest tent caterpillar (*Malacosoma disstria*) and the walnut caterpillar (*Datana integerrima*), which defoliate pecan trees; and the pecan carpenterworm (*Cossula magnifica*), found throughout the Eastern United States, whose larvae attack small twigs, bore into the pith, and soon burrow into heartwood. The pecan weevil (*Curculio caryae*) at times destroys most of the nut crop in the southern part of the pecan range. Heavy attacks by the obscure scale (*Chrysomphalus obscurus*) cause small limbs to die.

Pecan is susceptible to fire damage at all ages. Fire in the bottom lands moves rapidly along the soil surface, killing most tree reproduction and occasionally scorching the sensitive bark of older trees. Particularly hot fires may kill mature pecan trees.

Special Uses

Improved cultivars are extensively grown in the United States and abroad for commercial nut production. Pecan nuts are eaten by a number of birds, fox and gray squirrels, opossums, raccoons, and peccaries (37).

The demand for pecan wood has steadily increased in recent decades. It is used for furniture, cabinetry, panelling, pallets, and veneer. The wood has good machining properties, resembling those of true hickories (2,35).

Genetics

Population Differences

Studies of variation in natural pecan stands throughout Louisiana indicated a large genetic diversity within populations. Also, there was a high degree of variation between breeding populations, indicating a close relationship (inbreeding) among trees in small stands. Genotype × environment interaction was highly significant between progeny tests of open pollinated selected trees. Heritability estimates for height growth indicated ample genetic variation to anticipate significant gains in breeding programs (*1,28,29*).

Races and Hybrids

More than a hundred horticultural clones have been listed (*37*). These were selected primarily for various characteristics concerning commercial nut production. More recently several cultivars have been developed for the same purpose.

Complex hybridized natural populations are common. Natural interspecific hybridization occurs with *Carya aquatica* (*C.* × *lecontei* Little), *C. cordiformis* (*C.* × *brownii* Sarg.), *C. laciniosa* (*C.* × *nussbaumeri* Sarg.), *C. ovata*, and *C. tomentosa* (*C.* × *schneckii* Sarg.) (*17*).

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Carya laciniosa (Michx. f.) Loud. Shellbark Hickory

Juglandaceae **Walnut family**

Richard C. Schlesinger

Shellbark hickory (*Carya laciniosa*) is also called shagbark hickory, bigleaf shagbark hickory, kingnut, big shellbark, bottom shellbark, thick shellbark, and western shellbark, attesting to some of its characteristics. It is a slow-growing long-lived tree, hard to transplant because of its long taproot, and subject to insect damage. The nuts, largest of all hickory nuts, are sweet and edible. Wildlife and people harvest most of them; those remaining produce seedling trees readily. The wood is hard, heavy, strong, and very flexible, making it a favored wood for tool handles. A specimen tree has been reported in Missouri with 117 cm (46.2 in) in d.b.h., 36.9 m (121 ft) tall, and a spread of 22.6 m (74 ft).

Habitat

Native Range

Shellbark hickory (figs. 1,2) is widely distributed but is nowhere common. The range extends from western New York through southern Michigan to

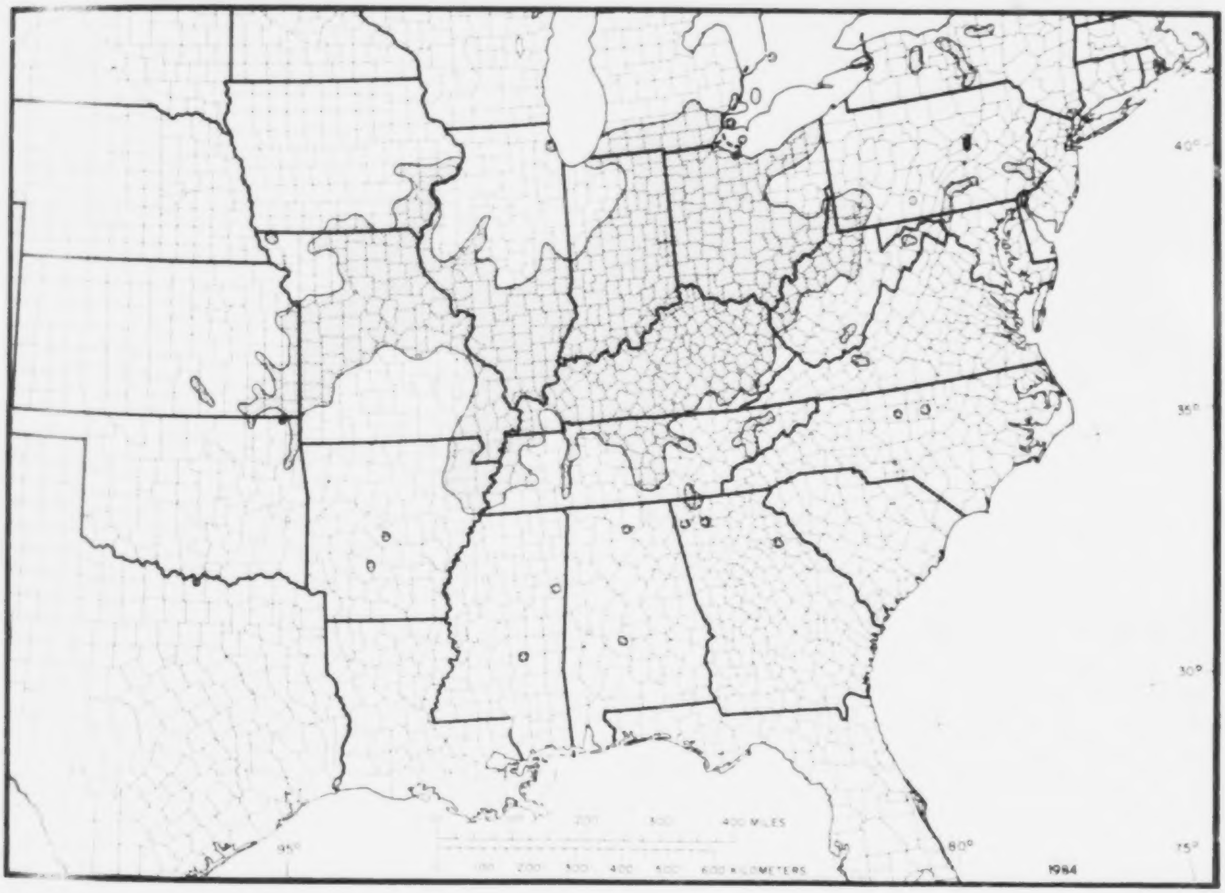

Figure 1—*The native range of shellbark hickory.*

The author is Principal Silviculturist, North Central Forest Experiment Station, St. Paul, MN.

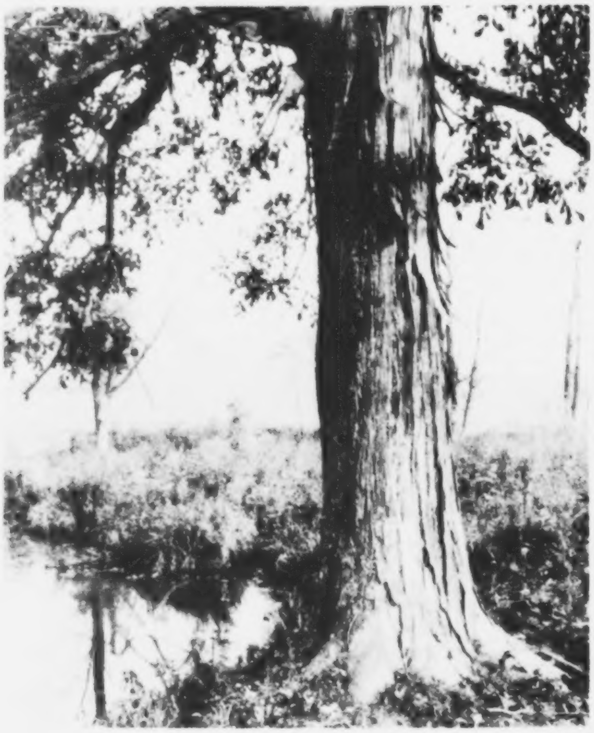

Figure 2—*Shellbark hickory.*

southeast Iowa, south through eastern Kansas into northern Oklahoma, and eastward through Tennessee into Pennsylvania. This species is most prominent in the lower Ohio River region and south along the Mississippi River to central Arkansas. It is frequently found in the great river swamps of central Missouri and the Wabash River region in Indiana and Ohio *(5)*.

Climate

The mean length of the frost-free period within the range of shellbark hickory is from 150 to 210 days. The average January temperature is between -4° and 5° C (25° and 41° F), and for July the mean temperature is from 23° to 27° C (73° to 81° F). An average minimum temperature of -26° C (-15° F) occurs in the northern part of the range, and an average maximum temperature of 38° C (100° F) is found throughout the range. Precipitation varies between 750 and 1500 mm (30 and 59 in) per year including 15 to 90 cm (6 to 35 in) of snow *(7)*.

Soils and Topography

Shellbark hickory grows best on deep, fertile, moist soils, most typical of the order Alfisols. It does not thrive in heavy clay soils but grows well on heavy loams or silt loams. Shellbark hickory requires moister situations than do pignut, mockernut or shagbark hickories *(Carya glabra, C. tomentosa,* or *C. ovata)*, although it is sometimes found on dry, sandy soils. Specific nutrient requirements are not known, but generally the hickories grow best on neutral or slightly alkaline soils.

The species is essentially a bottom-land species and is often found on river terraces and second bottoms. Land that is subject to shallow inundation for a few weeks early in the growing season is favorable for shellbark. However, the tree will grow on a wide range of topographic and physiographic sites *(7)*.

Associated Forest Cover

Shellbark hickory may be found in pure groups of several trees but is more frequent singly in association with other hardwoods. The species is a minor component of the forest cover types Bur Oak (Society of American Foresters Type 42), Pin Oak–Sweetgum (Type 65), and Swamp Chestnut Oak–Cherrybark Oak (Type 91). It may also be found in one or more of the types in which hickories are included, but it is not identified at the species level *(3)*.

Shellbark hickory commonly grows in association with American *(Ulmus americana)*, slippery *(U. rubra)*, and winged elms *(U. alata)*, white *(Fraxinus americana)* and green ash *(F. pennsylvanica)*, basswood *(Tilia americana)*, American hornbeam *(Carpinus caroliniana)*, red maple *(Acer rubrum)*, blackgum *(Nyssa sylvatica)*, sweetgum *(Liquidambar styraciflua)*, and cottonwood *(Populus deltoides)*. It is found in association with four other hickories—shagbark, mockernut, bitternut *(Carya cordiformis)*, and water *(C. aquatica)*, and numerous oak species including swamp white *(Quercus bicolor)*, pin *(Q. palustris)*, white *(Q. alba)*, Shumard *(Q. shumardii)*, water *(Q. nigra)*, Delta post *(Q. stellata* var. *paludosa)*, swamp chestnut *(Q. michauxii)*, and Nuttall *(Q. nuttallii)*.

The herbaceous stratum includes numerous sedges and grasses. The shrub and small tree layer may be composed of painted buckeye *(Aesculus sylvatica)*, pawpaw *(Asimina triloba)*, flowering dogwood *(Cornus florida)*, eastern redbud *(Cercis canadensis)*, possumhaw *(Ilex decidua)*, poison-ivy *(Toxicodendron radicans)*, and trumpet-creeper *(Campsis radicans)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Shellbark hickory is monoecious, producing flowers from April to June after the leaves appear. The male flowers develop from the axils of leaves of the previous season or from inner scales of the terminal buds at the base of the current growth. The female flowers appear in short spikes or peduncles terminating in shoots of the current year. The pollen is wind disseminated. The fruit ripens from September to November *(2)*.

Seed Production and Dissemination—Shellbark nuts are the largest produced by any hickory. The number of cleaned seed per kilogram ranges from 55 to 75 (25 to 35/lb). Hickories show embryo dormancy. Shellbark hickory seeds require from 90 to 120 days of cold stratification before they will germinate. The minimum tree age for seed production is about 40 years, with the most seed produced between 75 and 200 years. Thrifty trees may produce 70 to 105 liters (2 to 3 bu) of nuts in a good year, and good crops are produced about every second year *(2)*.

The seed is dispersed from September to December by gravity, birds, and animals. Squirrels and other rodents are the principal dispersal agents *(7)*.

Seedling Development—Shellbark hickory requires moist soil for good germination and establishment. Germination is hypogeal. Seeds germinate from late April to early June. The seedlings rapidly develop a long taproot, but shoot growth is initially slow. Shellbark hickory seedlings grow faster in height than most of the other hickories *(7)*.

Shellbark hickory is shade tolerant in early life and reproduces under forest conditions. Under light shade height growth may be slow. In the Ohio Valley, seedlings were only 11 cm (4 in) tall after 1 year and 56 cm (22 in) tall at the end of 5 years.

Vegetative Reproduction—Shellbark hickory sprouts readily when cut, and coppice management has been recommended for this and other hickories. It is a persistent sprouter following fire and/or grazing. Although more difficult to propagate by grafting and budding than fruit trees, this species can be reproduced by these techniques with good success. It is not known whether shellbark hickory will root from cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—The hickories as a group grow slowly in diameter, and shellbark hickory is no exception. Sapling size trees average 2 mm (0.08 in) per year in diameter growth, increasing to 3 mm (0.12 in) per year as poles and sawtimber. Second-growth trees show growth rates of 5 mm (0.20 in) per year. Shellbark hickory occasionally grows to a height of 40 m (131 ft) and a diameter of 100 cm (39 in) *(7)*.

Rooting Habit—Shellbark hickory develops a large taproot that penetrates deeply into the soil. Lateral roots emerge at nearly right angles to the taproot, spreading horizontally through the soil. No distinct major lateral roots develop. In Illinois, root growth was rapid in April, slowed during July and August, increased again in September, and ended in late November *(7)*.

Mycorrhizal associations are formed when trees are young. The only specific fungus identified from shellbark hickory roots is an ectotrophic mycorrhiza, *Laccaria ochropurpurea (8)*.

Reaction to Competition—Shellbark hickory is very shade tolerant, exceeded only by sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*). It grows slowly under a dense canopy, however. In stands with only partial shade, it reproduces well. It is a very strong competitor in most of the species associations in which it is found.

Under forest conditions, shellbark hickory often develops a clear bole for half its length and has a narrow, oblong crown. Open-grown trees have egg-shaped crowns *(7)*. Heavy release sometimes results in epicormic branching.

Damaging Agents—Although numerous insects and diseases affect hickories, shellbark hickory has no enemies that seriously threaten its development or perpetuation as a species. Seed production can be reduced significantly, however, through attack by several insects. Two of the most important are the pecan weevil (*Curculio caryae*) and the hickory shuckworm (*Laspeyresia caryana*).

The hickory bark beetle (*Scolytus quadrispinosus*) feeds in the cambium and seriously weakens or even kills some trees. Adults of the hickory spiral borer (*Agrilus arcuatus torquatus*) feed on leaves, but the larvae feed beneath the bark and can be very destructive to hickory seedlings. The flatheaded appletree borer (*Chrysobothris femorata*) likewise is a foliage feeder as an adult, but its larvae feed on the phloem and outer sapwood.

The living-hickory borer *(Goes pulcher)* feeds in the trunks and branches of trees. A twig girdler *(Oncideres cingulata)* can seriously affect reproduction by killing back the tops of seedlings and sprouts. Both standing dead trees and freshly cut logs are highly susceptible to attacks by numerous species of wood borers.

A large number of insect species feed on hickory foliage. None of them cause serious problems for shellbark hickory, although they may be responsible for some stem deformity and growth loss *(1)*.

Shellbark hickory is free of serious diseases, but it is a host species for a variety of fungi. More than 130 fungi have been identified from species of *Carya*. These include leaf disease, stem canker, wood rot, and root rot-causing fungi. Specific information for shellbark hickory is not available *(4)*.

Shellbark hickory is susceptible to bole injury from fire, and fire injuries are often invaded by wood rot fungi. It is resistant to snow and ice damage but is susceptible to frost damage.

Special Uses

Shellbark hickory nuts are used for food by ducks, quail, wild turkeys, squirrels, chipmunks, deer, foxes, raccoons, and white-footed mice. A few plantations of shellbark hickory have been established for nut production, but the nuts are difficult to crack even though the kernel is sweet. The wood is used for furniture, tool handles, sporting goods, veneer, fuelwood, and charcoal.

Genetics

Shellbark hickory hybridizes with pecan, *Carya illinoensis (C. × nussbaumeri* Sarg.), and shagbark hickory, *C. ovata (C. × dunbarii* Sarg.). Shellbark hickory has 32 chromosomes. In general, species within the genus with the same chromosome number are able to cross. Numerous hybrids among the *Carya* species with 32 chromosomes (pecan, bitternut, shellbark, and shagbark) have been described *(5,6)*.

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Carya myristiciformis (Michx. f.) Nutt. Nutmeg Hickory

Juglandaceae Walnut family

L. C. Maisenhelder and John K. Francis

Nutmeg hickory *(Carya myristiciformis)*, also called swamp hickory or bitter water hickory, is found as small, possibly relict populations across the South and in northern Mexico on rich moist soils of higher bottom lands and stream banks. Little is known of the growth rate of nutmeg hickory. Logs and lumber are sold mixed with other hickories. The nuts are an oil-rich food for wildlife.

Habitat

Native Range

Nutmeg hickory (figs. 1, 2) is scattered in a few areas in eastern South Carolina, central Alabama and Mississippi, northern Louisiana, southern Arkansas, eastern Texas, and northern Mexico. The

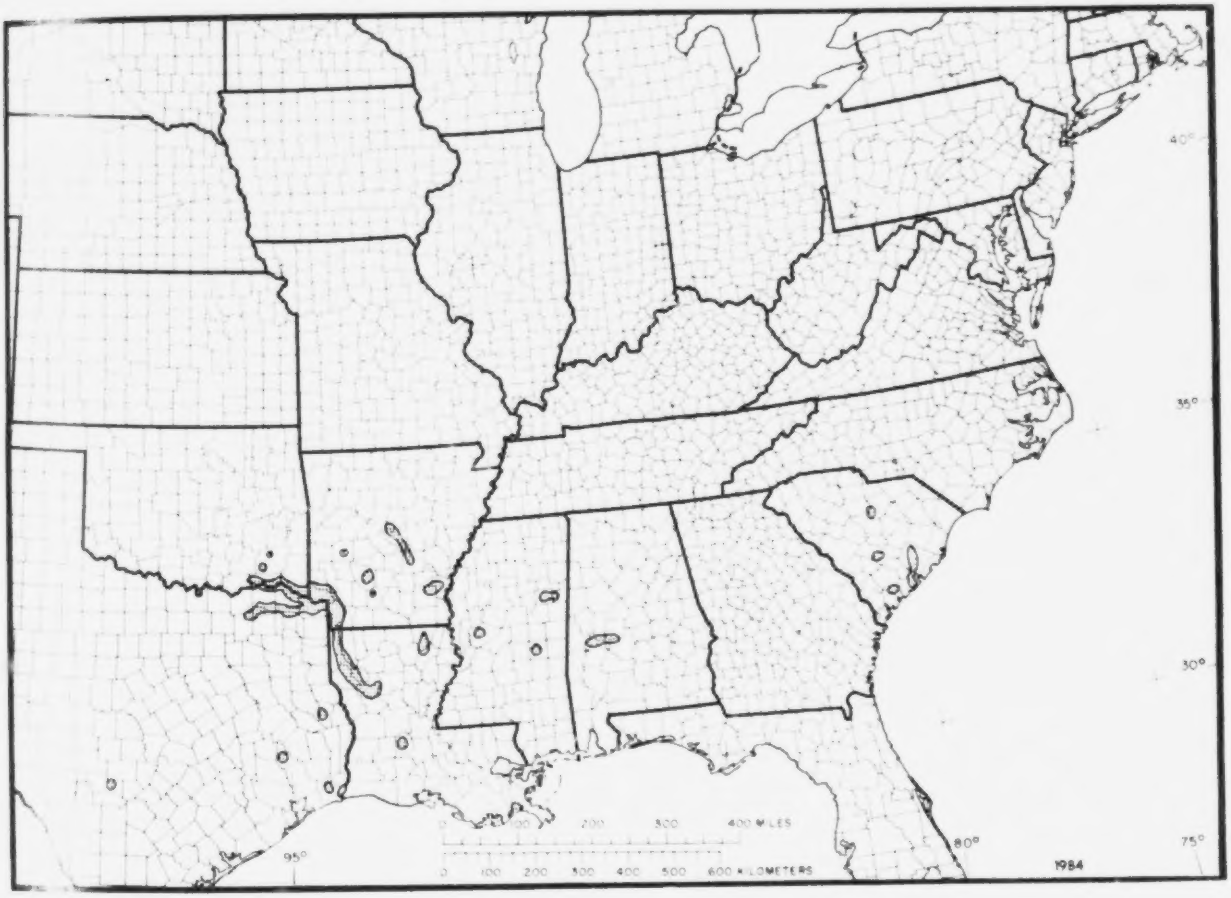

Figure 1—*The native range of nutmeg hickory.*

The authors are Silviculturist (deceased) and Soil Scientist, Southern Forest Experiment Station, New Orleans, LA. (Research on this species was done in cooperation with the University of Puerto Rico, Rio Piedras.)

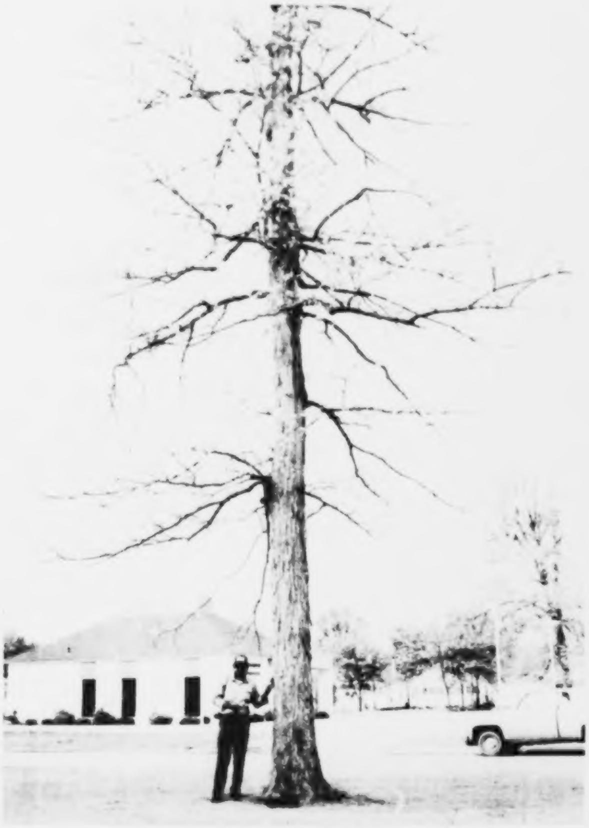

Figure 2—*Nutmeg hickory open grown in Desha County, AR.*

species is abundant only near Selma, AL, and in southern Arkansas. Nutmeg hickory has a native range nearly identical with that of Durand oak (*Q. durandii* var. *durandii*). Both may be relics of a more ancient flora than now occupies the region *(5)*.

Climate

Precipitation within the range of nutmeg hickory varies from 1020 to 1400 mm (40 to 55 in) per year, 510 mm (20 in) or more falling during the growing season. The frost-free period of most of the native range is about 240 days. Summers are warm and dry in the western portion of the range, but warm and wet in the South Carolina disjuncts. July temperatures average about 27° C (80° F). January temperatures average between 7° and 10° C (45° and 50° F). Extremes of temperature are -23° to 43° C (-10° to 110° F).

Soils and Topography

Nutmeg hickory grows on a variety of loamy, silty, or clayey soils that may be described as moist but well or moderately well drained and amply supplied with mineral nutrients. The species most often is found in minor stream bottoms, on second bottom flats, and on slopes or bluffs near streams. The principal soils on which nutmeg hickory is generally found are in the orders Alfisols and Inceptisols.

Associated Forest Cover

Nutmeg hickory is not an important species in any forest cover type and is only a minor associate in Swamp Chestnut Oak-Cherrybark Oak (Society of American Foresters Type 91) *(3)*. Other prominent associates in this type include white ash (*Fraxinus americana*); shagbark, shellbark, mockernut, and bitternut hickories (*Carya ovata, C. laciniosa, C. tomentosa, C. cordiformis*); Shumard oak (*Quercus shumardii*); and blackgum (*Nyssa sylvatica*). Less important associates are willow, water, and Durand oaks (*Q. phellos, Q. nigra, and Q. durandii*); American and winged elms (*Ulmus americana, U. alata*); yellow-poplar (*Liriodendron tulipifera*); and American beech (*Fagus grandifolia*). Some common small trees and shrubs occurring with nutmeg hickory are eastern hophornbeam (*Ostrya virginiana*), American hornbeam (*Carpinus caroliniana*), flowering dogwood (*Cornus florida*), and oakleaf hydrangea (*Hydrangea quercifolia*). One survey near Charleston, SC, found red buckeye (*Aesculus pavia*), eastern redbud (*Cercis canadensis*), and witch-hazel (*Hamamelis virginiana*) associated with nutmeg hickory *(5)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The species is monoecious and forms imperfect flowers. Both male and female flowers are found on the current year's growth. The male flowers are long-stalked catkins, developing at the shoot base *(7)*. The female flowers are in short spikes on peduncles at the end of the shoot. Flowering occurs from April to May, shortly after the leaves have started to open. Specifics of pollen production, dissemination and pollination are not known. The sweet, edible nut matures from September to October of the same year and falls between September and December. Its ellipsoidal shell is thick and hard.

Seed Production and Dissemination—Seed production starts when the trees are about 30 years old, and optimum seed-bearing age is 50 to 125 years *(5)*. Good seed crops are produced every 2 to 3 years. As many as 70 liters (2 bu) can be produced by an open-grown tree. Seeds are disseminated by various methods, including squirrels and water.

Seedling Development—The seeds of this species germinate from late April to early June. Germination is hypogeal. Burial of seeds by squirrels seems to be important, but it is not necessary for the successful establishment of seedlings.

Vegetative Reproduction—Specific information on the vegetative reproduction of nutmeg hickory is not available. Like other hickories, it probably sprouts readily from small stumps, injured or top-killed seedlings and saplings, and from roots *(2)*. Large stumps do not readily sprout, hence the larger the stump, the more likely that it will reproduce only by root suckers.

Sapling and Pole Stages to Maturity

Growth and Yield—Nutmeg hickory is a medium-sized tree with a tall, straight trunk and stout, slightly spreading branches that form a narrow and rather open crown. It can attain heights of 24 to 30 m (80 to 100 ft) and a diameter of 61 cm (24 in).

Although the pecan hickories (which include nutmeg hickory) grow more rapidly than the true hickories *(6)*, specific information on the growth rate of nutmeg hickory is lacking. The pecan hickories, in turn, grow more slowly than most other bottom-land hardwoods. The average 10-year diameter increase for hickories in natural, unmanaged stands in the northeast Louisiana delta was 4.3 cm (1.7 in) in the 15- to 30-cm (6- to 12-in) diameter class; 3.3 cm (1.3 in) in the 33- to 48-cm (13- to 19-in) diameter class; and 3.8 cm (1.5 in) in the 51- to 71-cm (20- to 28-in) diameter class *(5)*.

Pure stands of nutmeg hickory probably do not exist, and no volume figures are available. Logs and lumber from merchantable nutmeg hickory are sold mixed with other hickories.

Rooting Habit—Nutmeg hickory has a strongly developed taproot, especially on well-drained soil. Seedlings of hickory quickly develop a heavy taproot and fine lateral roots. During the pole stage, a robust, spreading lateral root system is developed.

Reaction to Competition—Nutmeg hickory is classed as intolerant of shade. It is intolerant as a mature tree, but tolerant in the seedling and sapling stage during which it may survive for a long time in the understory and then respond to release *(5)*. Any partial cutting system that removes larger, faster-growing competition encourages nutmeg hickory.

Damaging Agents—Fire damages hickory of all ages. A light burn kills the tops of seedlings and saplings; a more intense fire wounds larger trees and provides entry for butt-rotting fungi.

Several insects attack hickory but rarely become epidemic *(1)*. The forest tent caterpillar (*Malacosoma disstria*), walnut caterpillar (*Datana integerima*), and walkingstick (*Diapheromera femorata*) may defoliate individual trees or limbs. Sucking insects, including aphids (*Monellia* spp.), feed on the underside of leaves, causing them to curl and drop prematurely. The twig girdler (*Oncideres cingulata*) may seriously prune seedlings and even large trees by girdling the terminal and branches. The hickory bark beetle (*Scolytus quadrispinosus*) can be troublesome during dry years and periods of stress.

The ambrosia beetle (*Platypus* spp. and *Xyleborus* spp.) and powderpost beetles (*Lyctus* spp. and *Xylobiops basilaris*) often cause economic damage to logs and lumber during storage and air-drying.

No important diseases of hickory other than a number of wood rots have been reported. Bird peck defect, caused by the yellow-bellied sapsucker, is common and serious in nutmeg hickory.

Special Uses

The nuts of nutmeg hickory are relished by squirrels, which begin cutting them while they are still green *(4)*. Other rodents and wildlife also eat the nuts. The species is too rare over most of its range to be of major economic importance. The wood of this pecan hickory is slightly inferior in strength and toughness to that of the true or upland hickories, but owing to the small volumes involved and difficulty of distinguishing it from the true hickories, nutmeg hickory is not separated from them during logging.

Genetics

No racial varieties or hybrids have been reported for nutmeg hickory.

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Carya ovata (Mill.) K. Koch   Shagbark Hickory

Juglandaceae   Walnut family

David L. Graney

Shagbark hickory *(Carya ovata)* is probably the most distinctive of all the hickories because of its loose-plated bark. Common names include shellbark hickory, scalybark hickory, shagbark, and upland hickory. Shagbark hickory is evenly distributed throughout the Eastern States and, together with pignut hickory, furnishes the bulk of the commercial hickory. The tough resilient properties of the wood make it suitable for products subject to impact and stress. The sweet nuts, once a staple food for American Indians, provide food for wildlife.

Habitat

Native Range

Shagbark hickory (figs. 1,2) is found throughout most of the Eastern United States from southeastern Nebraska and southeastern Minnesota through southern Ontario and southern Quebec to southern Maine, southward to Georgia, Alabama, Mississippi, Louisiana, and eastern Texas, and disjunctly in the mountains of northeastern Mexico. It is largely absent from the southeastern and Gulf coastal plains and lower Mississippi Delta areas.

Climate

Shagbark hickory grows best in a humid climate. It is one of the hardiest of the hickory species, however, and has successfully adapted to a wide range of climatic conditions. Within shagbark's natural range, average annual rainfall varies from 760 to 2030 mm (30 to 80 in) with 510 to 1020 mm (20 to 40 in) of rainfall during the growing season. Average snowfall usually is less than 3 cm (1 in) in the southern and southwestern portion of the tree's range to 254 cm (100 in) or more in northern New York and southern Ontario.

Within the range of shagbark hickory average annual temperatures vary from 4° C (40° F) in the north to nearly 21° C (70° F) in southeastern Texas. Average January temperature varies from -9° to 13° C (16° to 55° F) while mean July temperature varies from 18° to 27° C (65° to 80° F). Extreme temperatures of -40° and 46° C (-40° and 115° F) have been recorded within shagbark's natural range. The average growing season also varies widely from about 140 days in the North to 260 days in the South.

Soils and Topography

Sites occupied by shagbark hickory vary greatly. In the North it is found on upland (often south-facing) slopes, while farther south it is more prevalent on soils of alluvial origin *(15,16)*. In the Ohio Valley, shagbark grows chiefly on north and east slopes of fertile uplands; in the Cumberland Mountains it is confined to the coves and the north and east slopes; and in Arkansas, Mississippi, and Louisiana it grows principally in river bottoms. Shagbark is found on better sites up to elevations of 910 m (3,000 ft) in the Blue Ridge Mountains of the Carolinas and on north- and east-facing benches at elevations above 610 m (2,000 ft) in northern Arkansas. In northern Arkansas, shagbark hickory is often very common on clayey soils derived from Mississippian and Pennsylvanian shale formations and may represent nearly half of the stocking of privately owned woodlots on these sites.

The range of shagbark hickory encompasses 7 soil orders and 14 suborders *(24)*. Ultisols are the dominant upland soils in the southern half of the shagbark range while Alfisols and Mollisols are primary soil orders in the northern portion of the range. The soils within shagbark's range are derived from a wide variety of parent materials—sedimentary and metaphoric rocks, glacial till, and loess. The soils also represent a wide range in soil fertility, such as Alfisols and Mollisols which are high in base saturation to Ultisols which are low. Shagbark hickory is sensitive to changes in soil fertility. In the northern part of its range, the species is found on a variety of upland sites; in the southern areas, it is more common in the more fertile bottom lands and on the better north- and east-facing upland sites.

Associated Forest Cover

Hickories are consistently present in the broad forest association commonly called oak-hickory but are not generally abundant *(20)*. Shagbark hickory is specifically listed as a minor component in six forest cover types *(7)*: Bur Oak (Society of American Foresters Type 42), Chestnut Oak (Type 44), White Oak-Black Oak-Northern Red Oak (Type 52), Pin Oak-Sweetgum (Type 65), Loblolly Pine-Hardwood (Type 82), and Swamp Chestnut Oak-Cherrybark

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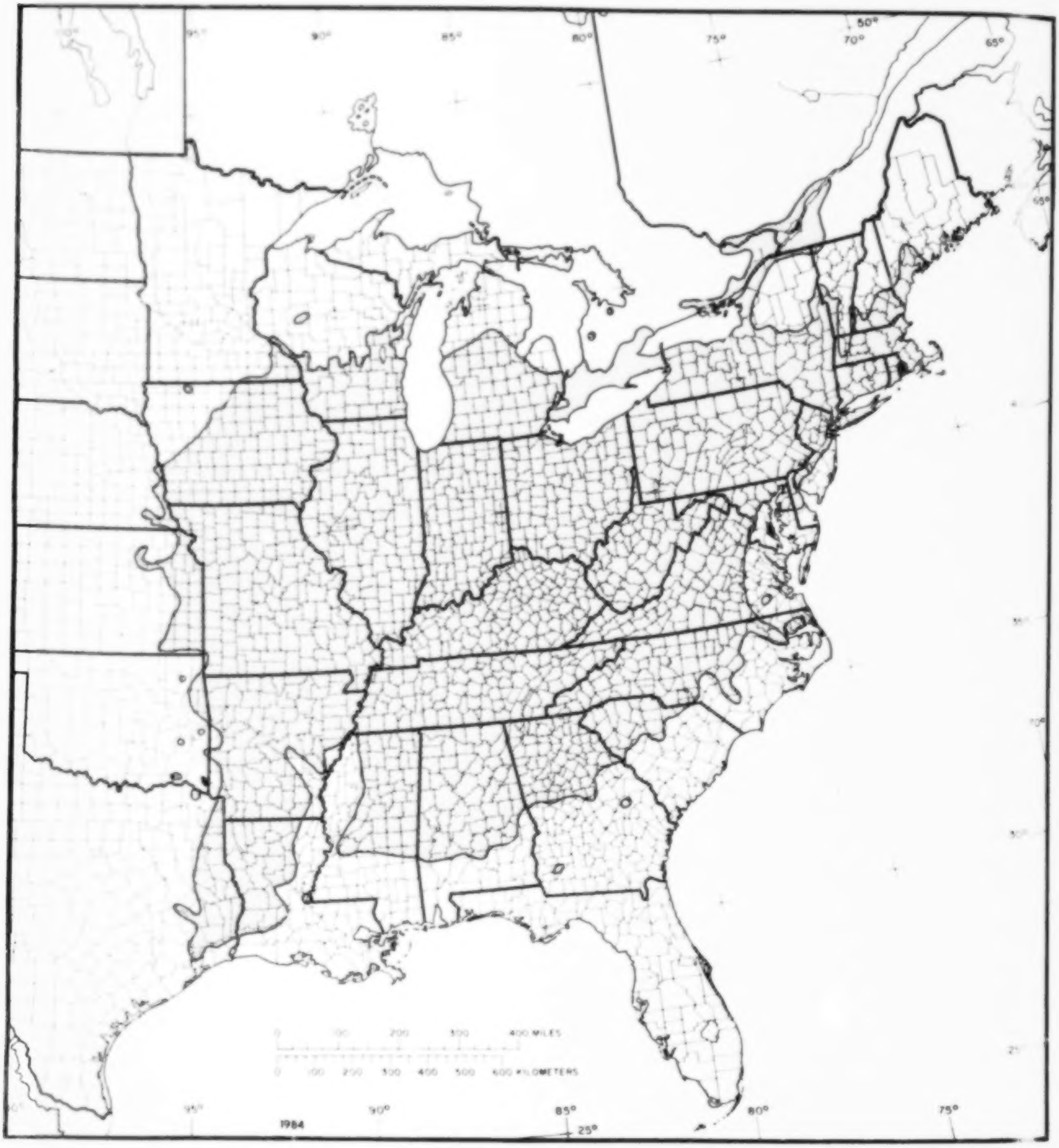
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Figure 1—*The native range of shagbark hickory.*

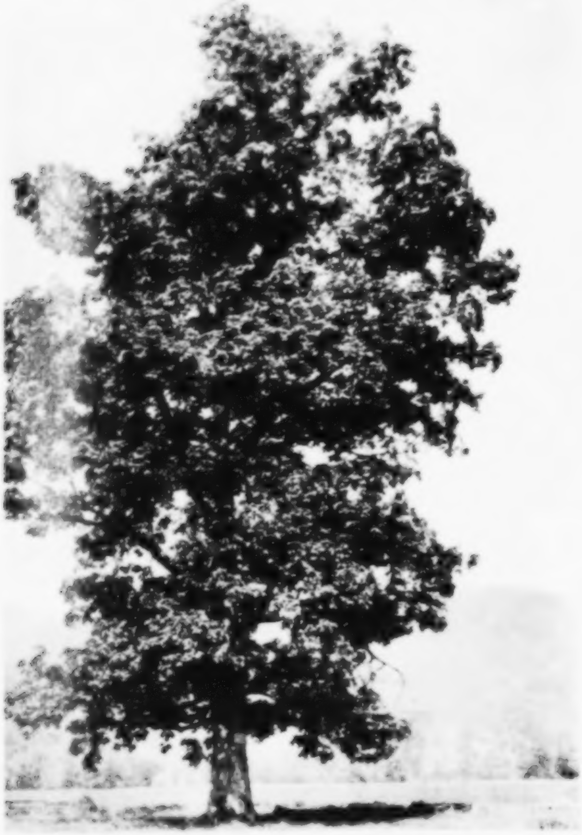

Figure 2—*Open grown shagbark hickory.*

Oak (Type 91). It is also a probable associate in the Eastern White Pine (Type 21), Beech–Sugar Maple (Type 60), White Oak (Type 53), and Northern Red Oak (Type 55) forest cover types. Through most of its range, shagbark hickory is associated with oaks, other hickories, and various mixed upland hardwoods. In the South it is also associated with a number of bottom-land hardwood species.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Shagbark hickory is monoecious and flowers in the spring. The staminate catkins are 10 to 15 cm (4 to 6 in) long and develop from axils of previous season leaves or from inner scales of the terminal buds at the base of the current growth. The pistillate flowers appear in short spikes about 8 mm (0.3 in) long on peduncles terminating in shoots of the current year. Flowers open when leaves are nearly full size in late March in the southwest to early June in the north and northeastern part of the range.

The fruit, a nut, is variable in size and shape. Borne 1 to 3 together, individual fruits are 3 to 6 cm (1 to 2.5 in) long, oval to subglobose or obovoid, depressed at the apex, and enclosed in a thin husk developed from the floral involucre. The fruit ripens in September and October and seeds are dispersed from September through December. Husks are green prior to maturity and turn brown to brownish black as they ripen. The husks become dry at maturity and split freely to the base into four valves along grooved sutures. The enclosed nut is light brownish white, oblong-ovate, somewhat compressed, usually prominently four-angled at the apex and rounded at the base (*25*). The shell is relatively thin and the kernel is sweet and edible. The bulk of the edible embryonic plant is cotyledonary tissue.

Seed Production and Dissemination—Shagbark hickory reaches commercial seedbearing age at 40 years. Although maximum seed production occurs from 60 to 200 years, some seed is produced up to 300 years (*16*). Good seed crops occur at intervals of 1 to 3 years with light crops or no seed during the intervening years. Tree diameter and crown size or surface are probably the best indicators of shagbark seed production. In southeastern Ohio, 6-year seed production of dominant and codominant shagbark hickory trees with mean d.b.h. of 20.7 cm (8.1 in) (age 60 years), 26.1 cm (10.3 in) (age 90 years) and 45.1 cm (17.8 in) (age 75 years) averaged 16, 36, and 225 sound seed per tree per year, respectively (*17*). Some individual shagbark trees have been known to produce 53 to 70 liters (1.5 to 2 bushels) of nuts during a good year (*4*). The germination of fresh seed is 50 to 75 percent.

Several species of insects influence seed production by causing aborting or premature dropping of fruits or by reducing the germinative capacity of mature nuts. Especially serious are the hickory shuckworm (*Laspeyresia caryana*), pecan weevil (*Curculio caryae*), and the hickorynut curculios (*Conotrachelus affinis* and *C. hicoriae*). In good seed years about half of the total seed crop is sound, but in years of low seed production, insect depredation could be proportionally higher, and a very low percentage of sound seed is produced (*17*).

Shagbark nuts are heavy, averaging about 220/kg (100/lb) and are disseminated primarily by gravity with some extension of seeding range caused by squirrels and chipmunks.

Seedling Development—Shagbark seeds show embryo dormancy that is overcome naturally by overwintering in the duff, or artificially by stratification in a moist medium or plastic bag at about 3° C (37° F) for 90 to 120 days *(3)*. Shagbark nuts should be stored in airtight containers at 5° C (41° F) and 90 percent relative humidity. Nuts stored longer than 2 years have lower germination percents and require only 60 days stratification *(3)*. In forest tree nurseries, unstratified nuts are sown in the fall and stratified nuts are sown in the spring. Mulching is recommended and protection from rodents is often required *(4)*. Germination is hypogeal.

Shagbark seedlings normally produce a long taproot and very little top growth during early development. In the Ohio Valley, 1-year-old seedlings grown in the open or under light shade in red clay soil produced an average root length of 0.3 (1 ft) and a top height of 7 cm (2.8 in). By age 3 the taproot extended to about 0.8 m (2.6 ft) while the top increased only to 19.8 cm (7.8 in) *(16)*.

Vegetative Reproduction—Shagbark hickory is a prolific sprouter. Nearly all of the cut or fire-killed hickories with stump diameters up to 20 to 24 cm (8 to 10 in) will produce sprouts. As stump diameters increase in size, stump sprouting declines, and proportion of root suckers increases *(16)*. Young hickory sprouts are vigorous and can maintain a competitive position in the canopy of a newly regenerated stand. After 10 to 20 years the rate of sprout height growth declines and hickory will normally lose crown position to the faster growing oaks and associated species.

Sapling and Pole Stages to Maturity

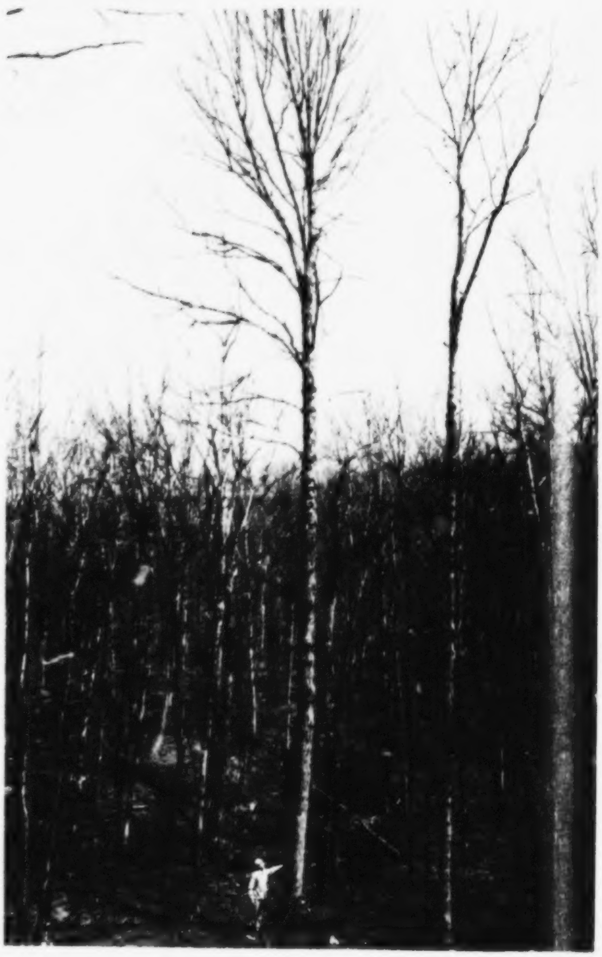

Figure 3—*Shagbark hickory in a mixed hardwood stand on a medium site. The larger tree is about 41 cm (16 in) in d.b.h. and 26 m (85 ft) tall.*

Growth and Yield—Shagbark hickory (fig. 3) is a medium-sized tree averaging 21 to 24 m (70 to 80 ft) tall, 30 to 61 cm (12 to 24 in) in d.b.h., and may reach heights of 40 m (130 ft) with a diameter of 122 cm (48 in). The tree characteristically develops a clear straight cylindrical bole, but there is a tendency for the main stem to fork at one-half to two-thirds of the tree height *(16)*. Although shagbark is one of the fastest growing hickories, its growth rates are less than most of the oaks and other associated species in upland stands. Representative height and d.b.h. by age are shown in table 1 for shagbark in different geographic areas. Regional volume tables for hickory trees and even-aged hickory stands are also available *(2,23)*. Hickory normally constitutes a small percentage of the stocking in upland hardwood stands and the most appropriate per acre yields of such stands are those presented by Schnur *(23)*, Gingrich *(8)*, and Dale *(5)*.

Rooting Habit—Shagbark seedlings typically develop a large and deep taproot with few laterals. The taproot may penetrate to a depth of 0.6 to 0.9 m (2 to 3 ft) in the first 3 years with a correspondingly slow growth of seedling shoots. Shagbark is rated as windfirm on most sites.

Reaction to Competition—Shagbark hickory is classed as intermediate in shade tolerance. Saplings and small reproduction persist under dense overstory

Table 1—Average diameter and height of shagbark hickory in selected geographic areas (adapted from *2*)

	D.b.h.	Height		
Age	S. Indiana and N. Kentucky[1]	Ohio Valley[1]	Cumberland Mountains[2]	Mississippi Valley[2]
yr	*cm*	*m*		
10	3	2.1	0.9	1.2
20	7	5.5	4.0	2.4
30	10	9.8	6.1	4.6
40	14	13.1	8.2	7.0
50	17	15.5	10.4	9.8
60	20	17.7	12.5	12.5
70	24	19.5	14.6	15.2
80	27	21.3	16.5	17.7
90	29	22.9	18.3	19.8
yr	*in*	*ft*		
10	1.2	7	3	4
20	2.8	18	13	8
30	4.0	32	20	15
40	5.4	43	27	23
50	6.8	51	34	32
60	8.0	58	41	41
70	9.4	64	48	50
80	10.5	70	54	58
90	11.6	75	60	65

[1] Second growth

[2] Virgin forest

canopies for many years and respond rapidly when released (*16*). It is a climax species in much of the oak-hickory forest area. The relatively slow growth habit of shagbark (and other hickories) places it at a distinct disadvantage under the even-aged management systems presently recommended for upland hardwood stands (if rotations are less than 100 years) (*19,20,21*). On most sites, height growth of hickory is slower than that of oaks and associated species and by midrotation the hickories are in the subdominant crown positions and become prime candidates for removal in periodic thinnings. Since hickories are long-lived trees and have the ability to withstand shade and crowding and respond when released, they are excellent species (along with white oak) for management on long rotations (200 or more years).

Damaging Agents—Shagbark hickory at all ages is susceptible to damage by fire. Light fires can result in top kill of reproduction and saplings (most of which later sprout). Hotter fires may kill larger trees and wound others, making them subject to butt rot and resultant degrade of lumber, loss of sound volume, or both (*15,16*). Holes made through the bark by sapsuckers (birdpeck) cause a discoloration of the wood that results in the rejection of a considerable amount of hickory lumber (*18*).

Hickories are affected by at least 133 known fungi and 10 other diseases (*9*). Most of the fungi are saprophytes but a few may cause damage to foliage, produce cankers, or cause trunk or root rots.

Canker rot caused by the fungus *Poria spiculosa* probably is the most widespread and serious of the diseases of the true hickories. Cankers form around dead branch stubs and the wood-rotting fungus can eventually spread throughout the heartwood. Though *P. spiculosa* is the most common trunk rot species, a large number of fungi will rot the living cylinder of hickories that have been injured by fire, logging damage, etc. (*9*).

Other common diseases of hickory are: anthracnose, (*Gnomonia caryae*) which causes irregular purplish- or reddish-brown spots on the upper leaf surface and dull brown spots beneath. These may merge to form irregular blotches and cause defoliation in wet seasons; mildew (*Microstroma juglandis*) invades leaves and twigs and may form witches' broom by stimulating bud formation; bunch disease (virus) also will cause witches' brooms similar in appearance to those of *M. juglandis*. The virus possibly is carried by sucking insects. Heavily affected trees may die prematurely. Crown gall (*Agrobacterium tumefaciens*) is a bacterial disease which causes tumors or wartlike aberrations on roots or at the base of the trunk, resulting eventually in a gradual decline and death of the tree. A gall-forming fungus species of *Phomopsis* can produce warty excrescences ranging from small twig galls to very large trunk burls.

At least 180 species of insects and mites are reported to infest hickory trees and wood products but few cause serious damage. The hickory bark beetle (*Scolytus quadrispinosus*) is the most important insect enemy of hickory and other hardwoods in the Eastern United States (*1*). During drought periods, outbreaks often develop in the Southeast, and large tracts of timber are killed. At other times, damage may be confined to single trees or tops of trees. The foliage of infested trees turns red within a few weeks after attack, and the trees soon die. Control measures include felling of infested trees and destroying the bark during the winter months or storing infested logs in ponds. To be effective, this type of control should be conducted over large areas.

The twig girdler (*Oncideres cingulata*) and twig pruner (*Elaphidionoides villosus*) often will severely prune heavily infested shade and park trees and can cause distortion in seedling and saplings in newly generated stands.

Special Uses

Hickories serve as food for many wildlife species. The nuts are a preferred food of squirrels and are eaten from the time fruits approach maturity in early August until the supply is gone. Hickory nuts also are 5 to 10 percent of the diet of eastern chipmunks. In addition to the mammals above, black bears, gray and red foxes, rabbits, and white-footed mice plus bird species such as mallards, wood ducks, bobwhites, and wild turkey utilize small amounts of hickory nuts *(14)*. Hickory is not a preferred forage species and seldom is browsed by deer when the range is in good condition. Hickory foliage is browsed by livestock only when other food is scarce.

The bark texture and open irregular branching of shagbark hickory make it a good specimen tree for naturalistic landscapes on large sites. It is an important shade tree in previously wooded residential areas. At least one ornamental cultivar of shagbark hickory has been reported *(10)*, but it is not planted as an ornamental to any great extent.

The species normally contributes only a very small percentage of total biomass of a given forest stand. Its adaptability to a wide range of site conditions and vigorous sprouting when cut make shagbark a candidate for coppice fuelwood. However, difficulty in planting and generally slow growth makes shagbark less attractive than many faster growing species.

Hickory has traditionally been very popular as a fuelwood and as a charcoal-producing wood. The general low percentage of hickory in the overstory of many privately owned woodlots is due in part to selective cutting of the hickory for fuelwood. Hickory fuelwood has a high heat value, burns evenly, and produces long-lasting steady heat; the charcoal gives food a hickory-smoked flavor.

The wood of the true hickories is known for its strength, and no commercial species of wood is equal to it in combined strength, toughness, hardness, and stiffness *(18)*. Dominant uses for hickory lumber are furniture, flooring, and tool handles. The combined strength, hardness, and shock resistance make it suitable for many specialty products such as ladder rungs, dowels, athletic goods, and gymnasium equipment.

Shagbark hickory is probably the primary species, after pecan *(Carya illinoensis)*, with potential for commercial nut production. The nuts have sweet kernels and fair cracking quality (which is often better in cultivars). The species can be successfully topgrafted on shagbark, and shellbark rootstocks and grafts on older rootstocks can bear in 3 to 4 years.

Genetics

Population Differences

Two varieties of shagbark hickory are recognized: *Carya ovata* var. *ovata*, which includes *C. mexicana* Engelm. ex Hemsl., and *C. ovata* var. *australis* (Ashe) Little, sometimes known as *C. carolinae-septentrionalis* (Ashe) Engl. & Graebner and often referred to as Carolina hickory or southern shagbark hickory *(11,12)*. The fruits are usually longer than 3.5 cm (1.4 in); the dark brown or black terminal bud scales and the generally lanceolate or oblanceolate terminal leaflets of var. *australis* serve to separate it from var. *ovata* with its smaller fruits (less than 3.5 cm (1.4 in) long), tan or light brown bud scales, and usually obovate terminal leaflets.

Races

Shagbark hickory shows a wide variety in morphological characteristics throughout its natural range and typically displays considerable diversity in nut size, shape, and color, as well as in shell thickness and in sweetness of the nutmeat *(16)*. Based on variability in size and shape of the nut and in character and amount of pubescence on leaves and branches, five additional varieties of *Carya ovata* were accepted in 1933 *(22)*, but none of these is recognized by more recent authors *(6,12)*.

Hybrids

Carya ovata is reported to hybridize with *C. laciniosa* (*C.* × *dunbarii* Sarg.) and *C. cordiformis* (*C.* × *laneyi* Sarg.), and a cross between shagbark and pecan has been recorded. There are five named clones of shagbark–pecan hybrids, three cultivars for shagbark–shellbark hybrids, and seven cultivars of shagbark–bitternut hybrids *(13)*.

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Carya tomentosa (Poir.) Nutt. Mockernut Hickory

Juglandaceae **Walnut family**

H. Clay Smith

Mockernut hickory (*Carya tomentosa*), also called mockernut, white hickory, whiteheart hickory, hognut, and bullnut, is the most abundant of the hickories. It is long lived, sometimes reaching the age of 500 years. A high percentage of the wood is used for products where strength, hardness, and flexibility are needed. It makes an excellent fuelwood, too.

Habitat

Native Range

Mockernut hickory (fig. 1), a true hickory, grows from Massachusetts and New York west to southern Ontario, southern Michigan, and northern Illinois; then to southeastern Iowa, Missouri, and eastern Kansas, south to eastern Texas and east to northern Florida. This species is not present in New Hampshire and Vermont as previously mapped by Little (*20*). Mockernut hickory is most abundant southward through Virginia, North Carolina, and Florida where it is the most common of the hickories. It is also abundant in the lower Mississippi Valley and grows largest in the lower Ohio River Basin and in Missouri and Arkansas (*24,26*).

Climate

The climate where mockernut hickory grows is usually humid. Within its range the mean annual precipitation measures from 890 mm (35 in) in the north to 2030 mm (80 in) in the south. During the growing season (April through September), annual precipitation varies from 510 to 890 mm (20 to 35 in). About 200 cm (80 in) of annual snowfall is common in the northern part of the range, but it seldom snows in the southern portion.

Annual temperatures range from 10° to 21° C (50° to 70° F). Temperatures range from 21° to 27° C (70° to 80° F) in July and from -7° to 16° C (20° to 60° F) in January. Temperature extremes are well above 38° C (100° F) and below -18° C (0° F). The growing season is approximately 160 days in the northern part of the range and up to 320 days in the southern part of the range (*33,37*).

Soils and Topography

In the north, mockernut hickory is found on drier soils of ridges and hillsides and less frequently on moist woodlands and alluvial bottoms (*26*). The species grows and develops best on deep, fertile soils (*11,24*). In the Cumberland Mountains and hills of southern Indiana, it grows on dry sites such as south and west slopes or dry ridges. Mockernut grows in Alabama and Mississippi on sandy soils with shortleaf pine (*Pinus echinata*) and loblolly pine (*P. taeda*). However, most of the merchantable mockernut grows on moderately fertile upland soils (*26*).

Mockernut hickory grows primarily on Ultisols occurring on an estimated 65 percent of its range, including much of the southern to northeastern United States (*36*). These soils are low in nutrients and usually moist, but during the warm season, they are dry part of the time. Along the mid-Atlantic and in the southern and western range, mockernut hickory grows on a variety of soils on slopes of 25 percent or less, including combinations of fine to coarse loams, clays, and well-drained quartz sands. On slopes steeper than 25 percent, mockernut often grows on coarse loams.

Mockernut grows on Inceptisols in an estimated 15 percent of its range. These clayey soils are moderate to high in nutrients and are primarily in the Appalachians on gentle to moderate slopes where water is available to plants during the growing season. In the northern Appalachians on slopes of 25 percent or less, mockernut hickory grows on poorly drained loams with a fragipan. In the central and southern Appalachians on slopes 25 percent or less, mockernut hickory grows on fine loams. On steeper slopes it grows on coarse loams (*36*).

In the northwestern part of the range, mockernut grows on Mollisols. These soils have a deep, fertile surface horizon greater than 25 cm (10 in) thick. Mollisols characteristically form under grass in climates with moderate to high seasonal precipitation.

Mockernut grows on a variety of soils including wet, fine loams, sandy textured soils that often have been burned, plowed, and pastured. Alfisols are also present in these areas and contain a medium to high supply of nutrients. Water is available to plants more than half the year or more than 3 consecutive months during the growing season. On slopes 25 percent or less, mockernut grows on wet to moist, fine loam soils with a high carbonate content (*36*).

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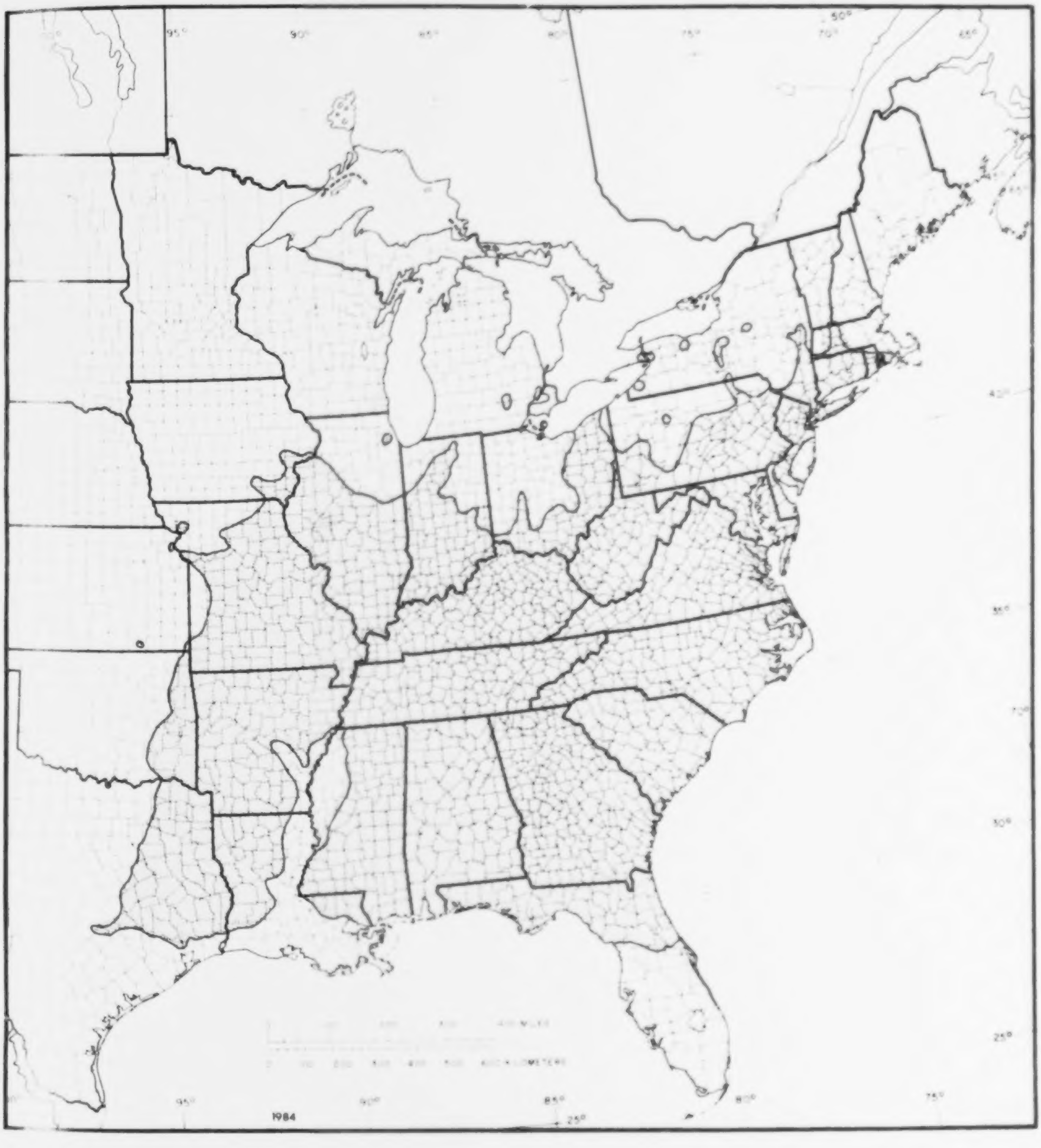
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Figure 1—*The native range of mockernut hickory*

Associated Forest Cover

Mockernut hickory is associated with the eastern oak-hickory forest and the beech-maple forest. The species does not exist in sufficient amounts to be included as a title species in the Society of American Foresters forest cover types *(9)*. Nevertheless, it is identified as an associated species in eight cover types. Three of the upland oak types and the bottom land type are subclimax to climax. The types are:

Central Forest Region (upland oaks)—Post Oak–Blackjack Oak (Type 40), White Oak–Black Oak–Northern Red Oak (Type 52), White Oak (Type 53), Black Oak (Type 110).

Southern Forest Region (southern yellow pines)—Shortleaf Pine (Type 75), Loblolly Pine–Shortleaf Pine (Type 80); (oak-pine type) Loblolly Pine–Hardwood (Type 82); (bottom-land type) Swamp Chestnut Oak–Cherrybark Oak (Type 91).

In the central forest upland oak types, mockernut is commonly associated with pignut hickory *(Carya glabra)*, shagbark hickory *(C. ovata)*, and bitternut hickory *(C. cordiformis)*; black oak *(Quercus velutina)*, scarlet oak *(Q. coccinea)*, chestnut oak *(Q. muehlenbergii)*, post oak *(Q. stellata)*, and bur oak *(Q. macrocarpa)*; blackgum *(Nyssa sylvatica)*, yellow-poplar *(Liriodendron tulipifera)*, maples *(Acer* spp.), white ash *(Fraxinus americana)*, eastern white pine *(Pinus strobus)*, and eastern hemlock *(Tsuga canadensis)*. Common understory vegetation includes flowering dogwood *(Cornus florida)*, sumac *(Rhus* spp.), sassafras *(Sassafras albidum)*, sourwood *(Oxydendrum arboreum)*, downy serviceberry *(Amelanchier* spp.), redbud *(Cercis canadensis)*, eastern hophornbeam *(Ostrya virginiana)*, and American hornbeam *(Carpinus caroliniana)*. Mockernut is also associated with wild grapes *(Vitis* spp.), rosebay rhododendron *(Rhododendron maximum)*, mountain-laurel *(Kalmia latifolia)*, greenbriers *(Smilax* spp.), blueberries *(Vaccinium* spp.), witch-hazel *(Hamamelis virginiana)*, and spicebush *(Lindera benzoin)*. Other understory vegetation includes New Jersey tea *(Ceanothus americanus)*, wild hydrangea *(Hydrangea arborescens)*, tick-trefoil *(Desmodium* spp.), bluestem *(Andropogon* spp.), poverty oatgrass *(Danthonia spicata)*, sedges *(Carex* spp.), pussytoes *(Antennaria* spp.), goldenrod *(Solidago* spp.), and asters *(Aster* spp.).

In the southern forest, mockernut grows with shortleaf pine, loblolly pine, pignut hickory, gums, several oaks, sourwood, and winged elm *(Ulmus alata)*. Other common understory vegetation includes flowering dogwood, redbud, sourwood, persimmon *(Diospyros virginiana)*, eastern redcedar *(Juniperus virginiana)*, sumacs, hawthorns *(Crataegus* spp.), blueberries, honeysuckle *(Lonicera* spp.), mountain-laurel, viburnums, greenbriers, and grapes.

In the Loblolly Pine–Hardwood Type in the southern forest, mockernut commonly grows in the upland and drier sites with white oak *(Quercus alba)*, post oak, northern red oak *(Q. rubra)*, southern red oak *(Q. falcata)*, and scarlet oak; shagbark and pignut hickories; and blackgum. Understory vegetation includes flowering dogwood, hawthorn, sourwood, greenbrier, grape, honeysuckle, and blueberry. In the southern bottom lands, mockernut occurs in the Swamp Chestnut Oak–Cherrybark Oak Type along with green ash *(Fraxinus pennsylvanica)*, white ash, shagbark, shellbark *(Carya laciniosa)*, and bitternut hickories; white oak, Delta post oak *(Quercus stellata* var. *paludosa)*, Shumard oak *(Q. shumardii)*, and blackgum. Understory trees include pawpaw *(Asimina triloba)*, flowering dogwood, painted buckeye *(Aesculus sylvatica)*, American hornbeam, devils-walking stick *(Aralia spinosa)*, redbud, American holly *(Ilex opaca)*, dwarf palmetto *(Sabal minor)*, and Coastal Plain willow *(Salix caroliniana)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Mockernut hickory is monoecious—male and female flowers are produced on the same tree. Mockernut male flowers are catkins about 10 to 13 cm (4 to 5 in) long and may be produced on branches from axils of leaves of the previous season or from the inner scales of the terminal buds at the base of the current growth *(4)*. The female flowers appear in short spikes on peduncles terminating in shoots of the current year. Flowers bloom in the spring from April to May, depending on latitude and weather. Usually the male flowers emerge before the female flowers. Hickories produce very large amounts of pollen that is dispersed by the wind.

Fruits are solitary or paired and globose, ripening in September and October, and are about 2.5 to 9.0 cm (1.0 to 3.5 in) long with a short necklike base. The fruit has a thick, four-ribbed husk 3 to 4 mm (0.11 to 0.16 in) thick that usually splits from the middle to the base. The nut is distinctly four-angled with a reddish-brown, very hard shell 5 to 6 mm (0.20 to 0.23 in) thick containing a small edible kernel *(4,10,19,22)*.

Seed Production and Dissemination—The seed is dispersed from September through December. Mockernut hickory requires a minimum of 25 years to reach commercial seed-bearing age. Optimum seed production occurs from 40 to 125 years, and the maximum age listed for commercial seed production is 200 years *(4)*.

Good seed crops occur every 2 to 3 years with light seed crops in intervening years. Approximately 50 to 75 percent of fresh seed will germinate *(26)*. Fourteen mockernut hickory trees in southeastern Ohio produced an average annual crop of 6,285 nuts for 6 years, about 39 percent were sound, 48 percent aborted, and 13 percent had insect damage *(28)*. Hickory shuckworm *(Laspeyresia caryana)* is probably a major factor in reducing germination.

Mockernut hickory produces one of the heaviest seeds of the hickory species; cleaned seeds range from 70 to 250 seeds/kg (32 to 113/lb). Seed is disseminated mainly by gravity and wildlife particularly squirrels. Birds also help disperse seed. Wildlife such as squirrels and chipmunks often bury the seed at some distance from the seed-bearing tree.

Seedling Development—Hickory seeds show embryo dormancy that can be overcome by stratification in a moist medium at 1° to 4° C (33° to 40° F) for 30 to 150 days. When stored for a year or more, seed may require stratification for only 30 to 60 days. Hickory nuts seldom remain viable in the ground for more than 1 year. Hickory species normally require a moderately moist seedbed for satisfactory seed germination, and mockernut hickory seems to reproduce best in moist duff. Germination is hypogeal.

Mockernut seedlings are not fast growing. The height growth of mockernut seedlings observed in the Ohio Valley in the open or under light shade on red clay soil was as follows *(24,26)*:

	Height	
yr	*cm*	*in*
1	8	3.0
2	12	4.7
3	20	8.0
4	32	12.5
5	51	20.0
6	71	28.0

Vegetative Reproduction—True hickories sprout prolifically from stumps after cutting and fire. As the stumps increase in size, the number of stumps that produce sprouts decreases *(27)*; age is probably directly correlated to stump size and sprouting. Coppice management is a possibility with true hickories. True hickories are difficult to reproduce from cuttings. Madden *(18)* discussed the techniques for selecting, packing, and storing hickory propagation wood. Reed *(30)* indicated that the most tested hickory species for root stock for pecan hickory grafts were mockernut and water hickory *(Carya aquatica)*. However, mockernut root stock grew slowly and reduced the growth of pecan tops. Also, this graft seldom produced a tree that bore well or yielded large nuts.

Sapling and Pole Stages to Maturity

Growth and Yield—Mockernut hickory (fig. 2) is a large, true hickory with a dense crown. This species occasionally grows to about 30 m (100 ft) tall and 91 cm (36 in) in d.b.h., but heights and diameters usually range from about 15 to 24 m (50 to 80 ft) and 46 to 61 cm (18 to 24 in), respectively.

The relation of height to age is as follows *(26)*:

Age	Height Cumberland Mountains		Mississippi Valley	
yr	*m*	*ft*	*m*	*ft*
10	1.2	4	2.7	9
20	5.2	17	5.5	18
30	7.9	26	7.6	25
40	10.1	33	9.1	30
60	13.7	45	12.2	40
80	16.8	55	14.9	49
100	20.1	66	17.4	57
120	23.2	76	19.8	65
160	28.7	94	24.4	80
200	33.2	109	29.0	95

The current annual growth of mockernut hickory on dry sites is estimated at about 1.0 m^3/ha (15 ft^3/acre). In fully stocked stands on moderately fertile soils, 2.1 m^3/ha (30 ft^3/acre) is estimated, though annual growth rates of 3.1 m^3/ha (44 ft^3/acre) were reported in Ohio *(26)*. Greenwood and bark weights for commercial-size mockernut trees from mixed hardwoods in Georgia are available for total tree and saw-log stems to a 4-inch top for trees 5 to 22 inches d.b.h. *(6)*.

Available growth data and other research information is summarized for hickory species, not for individual species. Trimble *(32)* compared growth rates of various Appalachian hardwoods including a hickory species category. Dominant-codominant hickory trees 38 to 51 cm (15 to 20 in) in d.b.h. on good oak sites grew slowly compared to northern red oak, yellow-poplar, black cherry *(Prunus serotina)*, and sugar maple *(Acer saccharum)*. Hickories were in the white oak, sweet birch *(Betula lenta)*, and American beech *(Fagus grandifolia)* growth-rate category. Dominant-codominant hickory trees grew about 3 mm (0.12 in) d.b.h. per year compared to 5 mm (0.20 in) for the moderate-growth species (black cherry) and 6 mm (0.23 in) for the faster growing species (yellow-poplar and red oak). Equations are available for predicting

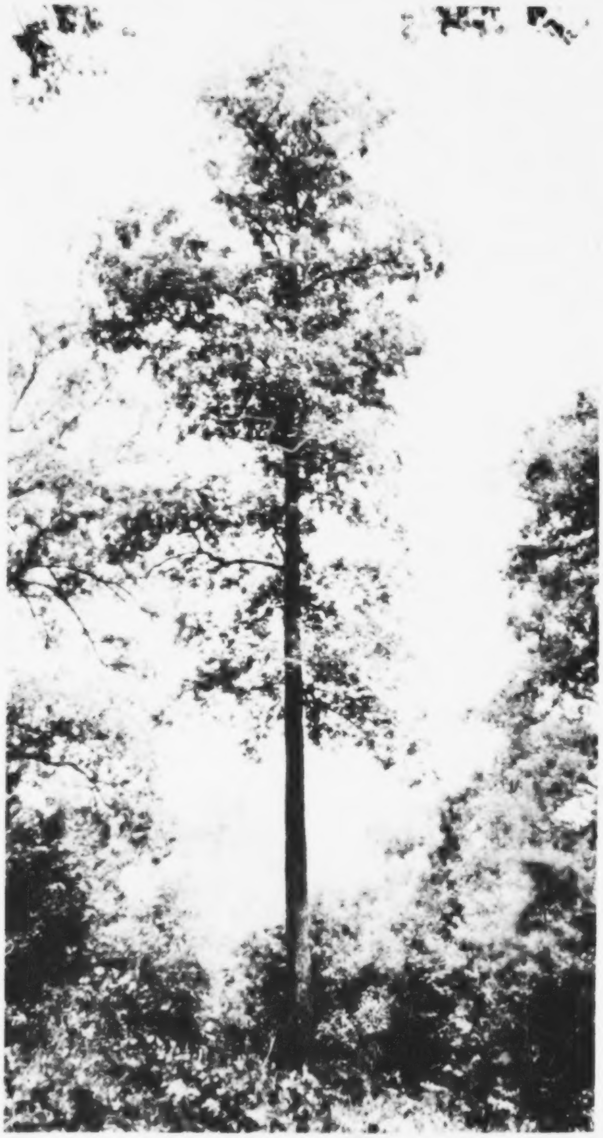

Figure 2—*A mockernut hickory 31 m (101 ft) tall and 56 cm (22 in) in d.b.h.*

merchantable gross volumes from hickory stump diameters in Ohio *(12)*. Also, procedures are described for predicting diameters and heights and for developing volume tables to any merchantable top diameter for hickory species in southern Illinois and West Virginia *(23,39)*. Generally, epicormic branching is not a problem with hickory species, but a few branches do occur *(31,32)*.

Rooting Habit—True hickories such as mockernut develop a long taproot with few laterals. The species is windfirm. Early root growth is primarily into the taproot, which typically reaches a depth of 30 to 91 cm (12 to 36 in) during the first year. Small laterals originate along the taproot, but many die back during the fall. During the second year, the taproot may reach a depth of 122 cm (48 in), and the laterals grow rapidly. After 5 years, the root system attains its maximum depth, and the horizontal spread of the roots is about double that of the crown. By age 10, the height is 4 times the depth of the taproot *(35)*.

Reaction to Competition—At certain times during its life, mockernut hickory may be variously classified as tolerant to intolerant *(1,32)*. Overall it is classified as intolerant of shade. It recovers rapidly from suppression and is probably a climax species on moist sites *(26)*.

Silvicultural practices for managing the oak-hickory type have been summarized *(38)*. Establishing the seedling origin of hickory trees is difficult because of seed predators. Although infrequent bumper seed crops usually provide some seedlings, seedling survival is poor under a dense canopy. Because of prolific sprouting ability, hickory reproduction can survive browsing, breakage, drought, and fire. Top dieback and resprouting may occur several times, each successive shoot reaching a larger size and developing a stronger root system than its predecessors *(15)*. By this process, hickory reproduction gradually accumulates and grows under moderately dense canopies, especially on sites dry enough to restrict reproduction of more tolerant but more fire or drought sensitive species.

Wherever adequate hickory advance reproduction occurs, clearcutting results in new sapling stands containing some hickories. It is difficult to attain reproduction if advance hickory regeneration is inadequate, however; then clearcutting will eliminate hickories except for stump sprouts. In theory, light thinnings or shelterwood cuts can be used to create advance hickory regeneration, but this has not been demonstrated.

Damaging Agents—Mockernut hickory is extremely sensitive to fire because of the low insulating capacity of the hard, flinty bark *(13,25)*. Mockernut is not subject to severe loss from disease. The main fungus of hickory is *Poria spiculosa*, a trunk rot. This fungus kills the bark, which produces a canker, causes heart rot and decay, and can seriously degrade the tree *(13)*. Mineral streaks and sapsucker-induced streaks also degrade the lumber. In general, the hard, strong, and durable wood of hickories makes them relatively resistant to decay fungi. Most fungi cause little, if any, decay in small, young trees (*3,5*).

Common foliage diseases include leaf mildew and witches' broom (*Microstroma juglandis*), leaf blotch (*Mycosphaerella dendroides*), and pecan scab (*Cladosporium effusum*). Mockernut hickory is host to anthracnose (*Gnomonia caryae*).

Nuts of all hickory species are susceptible to attack by the hickory nut weevil (*Curculio caryae*). Another weevil (*Conotrachelus aratus*) attacks young shoots and leaf petioles. The *Curculio* species are the most damaging and can destroy 65 percent of the hickory nut crop. Hickory shuckworms also damage nuts (*2*).

The bark beetle (*Scolytus quadrispinosus*) attacks mockernut hickory, especially in drought years and where hickory species are growing rapidly. The hickory spiral borer (*Argilus arcuatus torquatus*) and the pecan carpenterworm (*Cossula magnifica*) are also serious insect enemies of mockernut. The hickory bark beetle probably destroys more sawtimber-size mockernut trees than any other insect. The hickory spiral borer kills many seedlings and young trees, and the pecan carpenterworm degrades both trees and logs (*26*). The twig girdler (*Oncideres cingulata*) attacks both small and large trees; it seriously deforms trees by sawing branches. Sometimes these girdlers cut hickory seedlings near ground level.

Two casebearers (*Acrobasis caryivorella* and *A. juglandis*) feed on buds and leaves; later they bore into succulent hickory shoots. Larvae of *A. caryivorella* may destroy entire nut sets. The living-hickory borer (*Goes pulcher*) feeds on hickory boles and branches throughout the East. Borers commonly found on dying or dead hickory trees or cut logs include the banded hickory borer (*Knulliana cincta*) a long-horned beetle (*Saperda discoidea*), the apple twig borer (*Amphicerus bicaudatus*), the flatheaded ambrosia beetle (*Platypus compositus*), the red-headed ash borer (*Neoclytus acuminatus*), and the false powderpost beetle (*Scobicia bidentata*).

Severe damage to hickory lumber and manufactured hickory products is caused by powderpost beetles (*Lyctus* spp. and *Polycaon stoutii*). Gall insects (*Caryomyia* spp.) commonly infest leaves. The fruit-tree leafroller (*Archips argyrospila*) and the hickory leafroller (*Argyrotaenia juglandana*) are the most common leaf feeders. The giant bark aphid (*Longistigma caryae*) is common on hickory bark. This aphid usually feeds on twigs and can cause branch mortality. The European fruit lecanium (*Parthnolecanium corni*) is common on hickories (*2*).

Mockernut is not easily injured by ice glaze or snow but young seedlings are very susceptible to frost damage. Many birds and animals feed on the nuts of mockernut hickory. This feeding combined with insect and disease problems eliminates the annual nut production, except during bumper seed crop years.

Special Uses

Mockernuts are preferred mast for wildlife, particularly squirrels, which eat green nuts. Black bears, foxes, rabbits, beavers, and white-footed mice feed on the nuts, and sometimes the bark. The white-tailed deer browse on foliage and twigs and also feed on nuts. Hickory nuts are a minor source of food for ducks, quail, and turkey (*7,21*).

True hickories provide a very large portion of the high-grade hickory used by industry (*8*). Mockernut is used for lumber, pulpwood, charcoal, and other fuelwood products. Hickory species are preferred species for fuelwood consumption. Mockernut has the second highest heating value among the species of hickories (*29*). It can be used for veneer, but the low supply of logs of veneer quality is a limiting factor (*17*).

Mockernut hickory is used for tool handles requiring high shock resistance. It is used for ladder rungs, athletic goods, agricultural implements, dowels, gymnasium apparatus, poles, shafts, well pumps, and furniture. Lower grade lumber is used for pallets, blocking, and so on (*34*). Hickory sawdust, chips, and some solid wood are often used by packing companies to smoke meats, and mockernut is the preferred wood for smoking hams (*16*). Though mockernut kernels are edible, because of their size they are rarely eaten by humans.

Genetics

There is no published information concerning population or other genetic studies of this species.

Hickories are noted for their variability, and many natural hybrids are known among North American species. Hickories usually can be intercrossed successfully within the genus (*14*). Geneticists recognize that mockernut hickory hybridizes naturally with *C. illinoensis* (*Carya* × *schneckii* Sarg.) and *C. ovata* (*Carya* × *collina* Laughlin).

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Castanopsis chrysophylla (Dougl.) A. DC. Giant Chinkapin

Fagaceae Beech family

Arthur McKee

Giant chinkapin (*Castanopsis chrysophylla*), also called golden chinkapin, giant evergreen-chinkapin, and goldenleaf chestnut, is an interesting hardwood species in a landscape dominated by coniferous forests. Over much of its range, giant chinkapin shows several growth forms; it grows in a wide variety of habitats but is rarely a dominant component of any stand. In certain portions of its range, it can be an undesirable competitor of commercial species during early stages of stand development. Ecologically and taxonomically, it remains a poorly understood species.

Habitat

Native Range

The natural range of giant chinkapin (figs. 1, 2) extends from San Luis Obispo County in California to Mason County in west-central Washington (*14*). In California, it grows primarily in the Coast Ranges, with a disjunct population in the Sierra Nevada in El Dorado County (*8*). In Oregon, it is found in the Coast Ranges as far north as Benton County, and throughout the Cascade Range. Giant chinkapin is represented in Washington by two disjunct populations in Mason and Skamania Counties (*13*). Shrub forms of the species are found throughout its range. The tree form is primarily distributed from Lane County, OR, south to Marin County, CA. It is found from near sea level in the Coast Ranges of Oregon and California to over 1525 m (5,000 ft) in elevation in the Cascades. Although giant chinkapin is generally thought of as a mid- to low-elevation species, the shrub form can be found along the crest of the Cascade Range in Oregon from 1525 to 1830 m (5,000 to 6,000 ft) (*5*).

Climate

The generally mild climate over the range of giant chinkapin is characterized by winter precipitation and summer drought. Rainfall ranges from an annual mean of less than 510 mm (20 in) in southern California to more than 3300 mm (130 in) in the Cascades in Oregon. Much of the winter precipitation in the higher elevations of the Cascades occurs as snow. Little rain falls from June to September, and the duration and intensity of drought increase in the southern portion of the range, which has a Mediterranean climate.

The tree form of the species occurs in the warm but relatively moist portion of the climatic conditions within which it grows. Although the shrubby form is found throughout the species range, it achieves greatest coverage in the more extreme climates of xeric sites and higher elevations.

Soils and Topography

Giant chinkapin is found in a wide variety of topographic positions, from valley bottom to ridgetop, and on a wide range of soils. It achieves the highest cover in the northern portion of its range on Inceptisols and Entisols. In the southern portion of its range, highest cover is found on Inceptisols, Ultisols, and Alfisols. A partial list of parent materials includes basaltic, dioritic, sedimentary, metasedimentary, and serpentinaceous types. Giant chinkapin is ubiquitous in some portions of its range, such as the central part of the Cascades in Oregon, where it is a minor shrubby component of many forest stands on a range of soils. It achieves maximum size and cover, however, on sites that have relatively deep soils that apparently are deficient in nutrients (*17*).

In other portions of its range, giant chinkapin may be quite restricted, or its different growth forms may be found in markedly contrasting topographic and soil conditions. Nowhere is the latter more evident than in the Siskiyou and Klamath Mountains of southwestern Oregon and north coastal California, where the shrub form achieves greatest cover on dry, sterile, rocky ridgetops and southerly facing slopes in chaparral associations. The tree form is found on northerly aspects on benches and broad ridges with deep soils and more moderate moisture stresses (*2*).

Over much of the range of giant chinkapin, a general pattern emerges of a species that is at its competitive best on sites that are relatively infertile and droughty.

Associated Forest Cover

Pure stands of giant chinkapin are uncommon and rarely exceed 10 ha (25 acres). The species is a minor component in a wide range of forest communities and in its shrub form is a component of chaparral communities. Common tree associates in the Cascade

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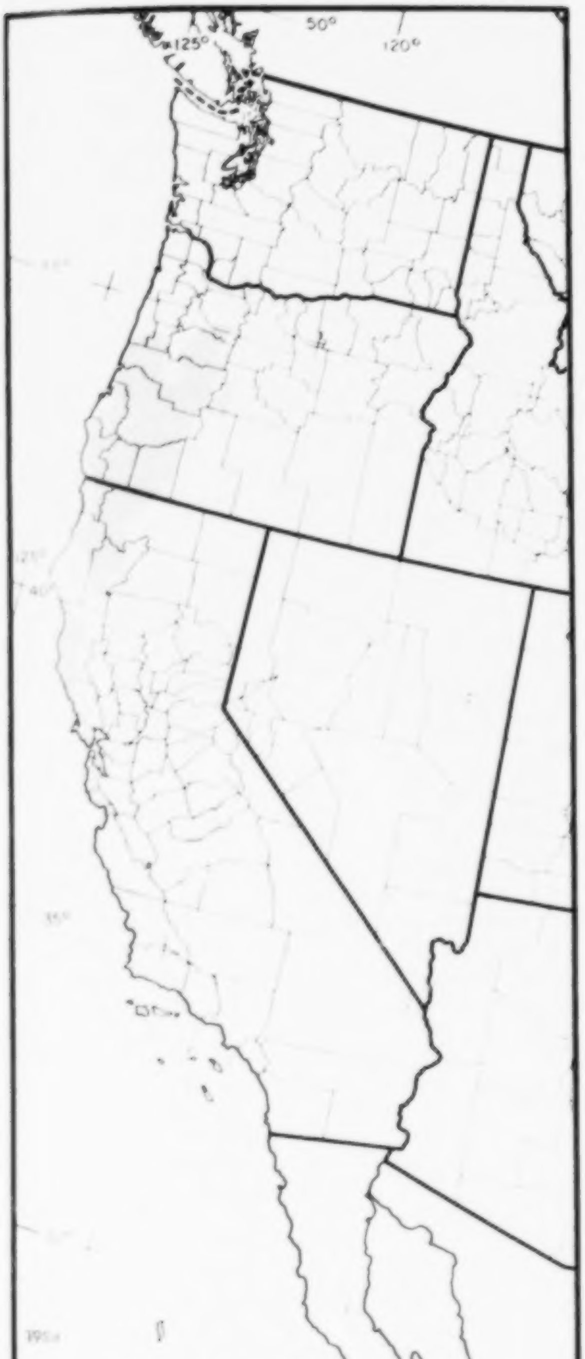

Figure 1—*The native range of giant chinkapin.*

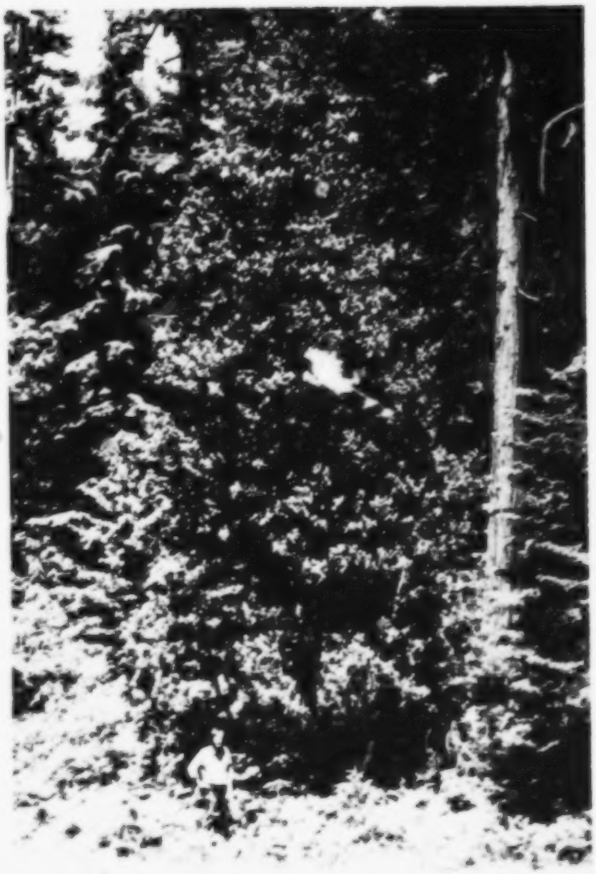

Figure 2—*Giant chinkapin approximately 35 years old*

Range are Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Libocedrus decurrens*), sugar pine (*Pinus lambertiana*), western hemlock (*Tsuga heterophylla*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), Pacific madrone (*Arbutus menziesii*), and Shasta red fir (*Abies magnifica* var. *shastensis*). In southwestern Oregon, Douglas-fir, western white pine (*Pinus monticola*), incense-cedar, sugar pine, Pacific madrone, and ponderosa pine continue to be associates, with the additional species: tanoak (*Lithocarpus densiflorus*), California black oak (*Quercus kelloggii*), knobcone pine (*Pinus attenuata*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), and canyon live oak (*Quercus chrysolepis*). Redwood (*Sequoia sempervirens*) is added to the list in north coastal California.

As a result of the wide ecological amplitude of both shrub and tree forms, giant chinkapin is found in many Society of American Foresters forest cover types (*3*). It is most important in terms of size and cover in certain communities in the following types: Pacific Douglas-Fir (Type 229), Douglas-Fir–Western Hemlock (Type 230); Port Orford-Cedar (Type 231); Sierra Nevada Mixed Conifer (Type 243), and Pacific Ponderosa Pine–Douglas-Fir (Type 244).

Common shrub species found in association with giant chinkapin in the Cascades in central Oregon are Pacific rhododendron (*Rhododendron macrophyllum*), salal (*Gaultheria shallon*), Oregongrape (*Berberis nervosa*), Pacific dogwood (*Cornus nuttallii*), and baldhip rose (*Rosa gymnocarpa*). Shrub associates in the Cascades in southern Oregon include: California dewberry (*Rubus ursinus*), baldhip rose, common snowberry (*Symphoricarpos albus*), salal, and ocean-spray (*Holodiscus discolor*). In southwestern Oregon, common shrub associates are: canyon live oak, huckleberry oak (*Quercus vaccinifolia*), poison-oak (*Rhus diversiloba*), Oregongrape, baldhip rose, California hazel (*Corylus cornuta* var. *californica*), California dewberry, and a number of manzanita (*Arctostaphylos*) species. Low shrub and herb species that are common associates include: modest whipplea (*Whipplea modesta*), common prince's-pine (*Chimaphila umbellata*), American twinflower (*Linnaea borealis*), bracken (*Pteridium aquilinum*), and common beargrass (*Xerophyllum tenax*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Giant chinkapin is monoecious, with unisexual staminate and pistillate flowers on the same plant. The staminate flowers form dense catkins 2.5 to 7.6 cm (1 to 3 in) long. One to three pistillate flowers are borne within an involucre at the base of the staminate catkin or separately along the stem. Pollination is adapted to wind, but bees frequent the flowers and probably aid in pollination, much to the dismay of beekeepers, for it imparts a bad taste to the honey in a mast year.

The fruit matures in the fall of the second growing season and contains one to three hard-shelled nuts within a very spiny golden brown bur 15 to 25 mm (0.6 to 1.0 in) broad, colloquially referred to as "porkypine eggs." The nuts are relatively large—1,800 to 2,400/kg (830 to 1,100/lb) *(11)*.

The phenology of flowering, fruit ripening, and seed dispersal varies widely over the range of giant chinkapin: flowering (February to July), fruit ripening (August to October), seed dispersal (fall). Three years of phenological records at the H. J. Andrews Experimental Forest in Oregon show local phenology to be less varied: flowering (mid-June to mid-July), fruit ripening (mid-August to early September), and seed dispersal (peaking in late September, but prolonged into early December).

Seed Production and Dissemination—Vigorously growing giant chinkapin produce some seed every year with mast years occurring at 2 to 5-year intervals. Understory shrubs of the species flower infrequently. Sound seeds are produced by vigorous trees, apparently of seed origin, that are 40 to 50 years old, but the age of the first seed production is probably much less. Six-year-old stump sprouts have produced some sound seeds.

The production of sound seeds can be greatly reduced locally by insects. In a sample of seeds at three locations in the H. J. Andrews Experimental Forest, two sites had less than 15 percent of the seeds infested, but at the third site nearly 100 percent of the seeds had been attacked by insects.

The primary agents of dissemination of giant chinkapin seed are gravity, squirrels, and birds, not necessarily in that order of importance. Vertebrates are undoubtedly important vectors. Several species of birds feed on nuts, and clumps of young seedlings not originating from sprouts implicate squirrels in caching food.

Seedling Development—Reported germination ranges from 14 to 53 percent *(11)*; one study found it to have the poorest rate of germination of all hardwoods in the Klamath Province of southwestern Oregon and northern California *(15)*. Germination is hypogeal and takes place in 16 to 24 days. Although the rate of germination was not increased by cold stratification, which suggested that germination and establishment in the fall are possible, no such germination was observed during 3 years of study at the H. J. Andrews Experimental Forest. Natural seedlings of giant chinkapin which ranged from 15 to 45 cm (6 to 18 in) in height were found only in relatively open stand conditions in the Experimental Forest. The individuals appeared to have germinated under a light leaf mulch in partial shade. The tallest was 12 years old and the shortest 4, but the height-age relationship was poor. In the northern Coast Ranges of California, the best seedling establishment occurs on mesic sites without dense layers of understory vegetation *(12)*.

Vegetative Reproduction—Giant chinkapin sprouts prolifically when cut or injured. Light understory fires cause vigorous basal sprouting. Even intense broadcast burns will not prevent basal sprouts from rapidly regrowing. Height growth of the sprouts can be rapid, outstripping young conifer growth for several years. Because of its aggressive sprouting ability, giant chinkapin is a problem for forest management on many sites.

The species is well adapted to a regime of frequent fires, which is reflected in the chaparral shrub form. Also, over much of the northern portion of the range of giant chinkapin, the tree form occupies ridgetop positions with other fire-adapted species. Its ability to exist with the potentially taller conifers may be the result of both its sprouting ability and relatively high fire frequency.

Sapling and Pole Stages to Maturity

Growth and Yield—Giant chinkapin is rarely a dominant species in a stand, and it is often an understory shrub or small tree of poor form. Growth and yield data are therefore nearly nonexistent for giant chinkapin despite its ability to develop a bole of good form and height in dense stands on optimum sites. The following information was obtained from unpublished data of the USDA Forest Service and Oregon State University.

Giant chinkapin provided 11 percent of the total stemwood volume of about 700 m^3/ha (50,000 fbm/acre) in an 80-year-old stand in the Coast Ranges of Oregon; the stand was site III for Douglas-fir. The mean diameter at breast height (d.b.h.) of stems greater than 15 cm (6 in) for giant chinkapin was 34 cm (13.4 in). The largest giant chinkapin in the stand were codominants about 27 m (90 ft) tall.

In two stands about 100 years old in the Cascades of Oregon, giant chinkapin made up 11 and 21 percent of the total stemwood volume. The two sites were site III and IV for Douglas-fir and had estimated volumes of about 800 and 550 m^3/ha (57,100 and 39,300 fbm/acre). In the site III stand, giant chinkapin stems greater than 10 cm (4 in) in d.b.h. averaged 20 cm (7.8 in) in d.b.h. Their mean diameter increment for the previous 10-year period was 1.8 mm (0.07 in) per year.

The average d.b.h. of giant chinkapin stems greater than 10 cm (4 in) in d.b.h. in the second stand on the poorer site was larger—30 cm (11.8 in). The mean annual diameter increment for the previous 10-year period was also slightly larger—2 mm (0.08 in) per year.

Because of the species' ability to resprout, individual genets of giant chinkapin could be several centuries old. The species is susceptible to heart-rotting fungi, which makes aging of large, old trees difficult. At the H. J. Andrews Experimental Forest in Oregon, the maximum age was found to range from 130 to 150 years. In the northern Coast Ranges of California maximum ages were estimated to range between 400 and 500 years, with the oldest trees on the more xeric habitats (*12*).

Rooting Habit—No information available.

Reaction to Competition—The competitive ability of giant chinkapin appears to be improved relative to its associates on nutritionally poor sites with high moisture stress. The shrub form is quite tolerant of shade. The tree form is less tolerant of shade and is probably most accurately classified as intermediate in tolerance, comparable to incense-cedar or sugar pine with which it is often found. Chinkapin does not attain the height of many of its associates, is often overtopped in mature stands of conifers, and declines in importance during later stages of succession. Over much of its range, some disturbance—such as fire, logging, or windstorm—is required for giant chinkapin to remain an important component of the forest on most sites. Under relatively droughty, infertile conditions, it can be a very aggressive and undesirable species during early succession. This is the aspect of giant chinkapin that is perhaps best known by foresters. Considerably more research has been conducted on how to rid sites of giant chinkapin than on how to promote its establishment and growth.

The most effective site preparation methods for controlling giant chinkapin have been scarification by tractor or spraying and burning. Neither slash burning nor hand scalping is effective, and herbicides produce only moderate results (*1,2,7*).

Because giant chinkapin is usually found mixed with other undesirable species, broad-spectrum herbicides, such as 2,4-D and triclopyr ester, have been used most frequently (*1,2,7*). Formulations of triclopyr ester have proven the most successful for both aerial and ground applications, including basal and stem treatment (*1,2*). The registration status of herbicides is subject to change. Consultation with local extension agents is advised when considering herbicide use.

Damaging Agents—Few diseases or insects are reported to affect growth and survival of giant chinkapin (*6,9*), but it is susceptible to heart-rotting fungi, such as *Phellinus igniarius* (*9*). It is resistant to chestnut blight (*Cryphonectria parasitica*) despite its close relationship to chestnut. Common leaf fungi appear to do little harm. Twig fungi are reported to be secondary to other agents of damage, and root and butt rots are rare.

Although in general giant chinkapin has few insect pests, seed-infesting species, such as the filbertworm (*Melissopus latiferreanus*), may play a significant local role in impeding regeneration. In portions of its range, certain foliage feeders, such as California oakworm (*Phryganidia californica*), can reduce growth. The roundheaded borer (*Phymatodes aeneus*) is occasionally found in dying branches and thin-barked portions of the bole (*6*).

Special Uses

A small market exists for giant chinkapin wood for furniture and cabinet stock, paneling, and decorative veneer (*16*). There are several reasons for its limited use, despite its ability to develop a tall, clear, straight bole under average growing conditions. It rarely occurs naturally in pure stands, being typically a minor hardwood component of predominantly coniferous forests. Also, most mills in the conifer-dominated industry of the Pacific States will not take giant chinkapin because of added inventory problems for little additional volume. Finally, it is one of the most difficult hardwoods in the United States to cure, as it tends to check badly (*16*), and transportation costs keep it from being moved long distances to the few mills equipped to process it. As a consequence, giant chinkapin is often felled and left on the site or is bucked into firewood.

Giant chinkapin is an important species for wildlife because of the cover and food it provides. Its ability to grow on harsh sites on infertile soils, and to sprout rapidly after fire, also makes it important for soil stabilization in watersheds.

Genetics

If much of the earlier discussion seemed to deal with two or perhaps three species, it may be because the taxonomy of the genus is poorly understood. Only 2 of about 150 species of *Castanopsis* are found in North America. These two are distinct from their Asian relatives, and systematists have created a new genus for them, *Chrysolepis* (*4,10*). The American species have a floral morphology that is intermediate to *Castanopsis* and *Lithocarpus*, and it represents the ancient condition of the family Fagaceae. The new scientific names for the American species, with the older names in parentheses, are *Chrysolepis chrysophylla* (Dougl.) Hjelmqvist (*Castanopsis chrysophylla* (Dougl.) A. DC.) for giant chinkapin and *Chrysolepis sempervirens* (Kell.) Hjelmqvist (*Castanopsis sempervirens* Dudl.) for evergreen chinkapin.

The uniqueness of the two species at the genus level does not imply a simple relationship between them. The ranges of the shrub form of giant chinkapin and of evergreen chinkapin overlap from northern coastal California into the Cascade Range of Oregon. The two species probably hybridize where they coexist (*8*). An apparently continuous intergradation of characters can be found in the Cascades in southern Oregon and in the Siskiyou Mountains.

The two growth forms of giant chinkapin are probably not the result of plastic phenotypic response to site conditions, although they may be in portions of the species range. In the northern Coast Ranges of California, the tree form occupies relatively moist conditions; the shrub form grows on dry, sterile ridgetops in chapparal communities. In the central part of the Cascades of Oregon, the pattern is reversed—the tree form is found primarily in relatively open and dry ridgetop forest communities, and the shrub form is spread through the more mesic forest stands. Only the shrub form is found at high elevations in the Cascade Range.

This variation is due to the probable existence of at least three ecotypes of giant chinkapin: a dry-site chaparral shrub ecotype of southwestern Oregon and northwestern California that probably matches the taxonomic category of *Castanopsis chrysophylla* var. *minor* Benth; a high-elevation ecotype adapted to heavy snowpack, cool temperatures, and short growing seasons found along the Oregon Cascades and in eastern Oregon; and a tree form that occurs in forest stands at lower elevations. The latter ecotype seems well adapted to dry, relatively infertile sites but can and does do well in more mesic conditions that have a history of disturbance by fire.

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Casuarina L. ex Adans Casuarina

Casuarinaceae Casuarina family

D. L. Rockwood, R. F. Fisher, L. F. Conde, and J. B. Huffman

Casuarina species, native to Australia and neighboring areas, have been introduced into many countries. In the United States, three species have been established, primarily in Hawaii, California, and Florida: *C. equisetifolia* L. ex J. R. & G. Forst., *C. cunninghamiana* Miq. and *C. glauca* Sieber ex K. Spreng. Other common names of *Casuarina* are Australian-pine, beefwood, and horsetail-tree.

Habitat

Range

Casuarina equisetifolia and *C. cunninghamiana* are naturalized to the southwestern and southeastern coastal areas of Florida as far north as Tampa and Titusville, with *C. equisetifolia* particularly prevalent on beaches; *C. glauca* is present throughout the same general area, frequently as very dense stands along roads and fence lines. *Casuarina cunninghamiana* exists as planted trees as far north as Gainesville. In Hawaii, *C. equisetifolia* is common along sandy coasts and lowlands *(9)*.

Climate

In Australia, these species grow in the tropical and subtropical north and east: *C. cunninghamiana* along rivers, *C. glauca* in swamps, and *C. equisetifolia* along the coast.

In Florida, *C. cunninghamiana* and *C. glauca* have a wide tolerance for moisture regimes, as they are present on sites ranging from dry to very wet but not permanently flooded. *Casuarina equisetifolia* performs well on dry sites only; *C. glauca* appears to be the most frost hardy, although it will not withstand long periods below freezing, and *C. cunninghamiana* is intermediate in frost tolerance. There seem to be no climatic barriers to sexual reproduction.

Soils and Topography

All three *Casuarina* species prefer coarse-textured soils of the Entisol, Inceptisol, and Spodosol orders. They show wide latitude in their soil demands and range from dry, sandy beach ridges to wet lake margins, but they withstand inundation for short periods only. In southeastern Florida, the species are particularly prevalent on alkaline, limestone-derived soils. *Casuarina equisetifolia* is tolerant of very saline conditions but grows best in slightly acid sandy soils. All three species tolerate low soil fertility but are quite responsive to fertilization with phosphorus or nitrogen and phosphorus. They reach maximum development in slightly depressional topography where adequate moisture is nearly always available.

Associated Forest Cover

When casuarina is present through natural seeding in Florida, it tends to form pure stands that are often nearly devoid of other vegetation *(4)*. It may coexist with vegetation such as Florida fishpoison-tree (*Piscidia piscipula*), button-mangrove (*Conocarpus erectus*), myrsine (*Rapanea punctata*), stopper (*Eugenia* spp.), randia (*Randia* spp.), cocoplum (*Chrysobalanus icaco*), southern bayberry (*Myrica cerifera*), redbay (*Persea borbonia*), and Florida poisontree (*Metopium toxiferum*) *(3)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Casuarina species have been reported to be monoecious *(13)* and dioecious *(6)*; *C. glauca* in Florida has not been observed to bear female flowers. Flowering occurs principally from April to June, with numerous minute narrow and terminal male flowers crowded in rings among grayish scales, and rounded and lateral female flowers occurring in light-brown clusters *(9, 13)*. Female flowers are wind pollinated. The multiple fruit, gray brown and 8 to 15 mm (0.3 to 0.6 in) in diameter, ripen from September through December. Seed bearing usually begins by age 5, and good seed crops occur annually *(13)*.

Seed Production and Dissemination—The conelike fruits mature throughout the year, although heavier crops occur in the fall and winter. When the fruits dry from December to March, the samaras, which range in length from 3 to 8 mm (0.1 to 0.3 in), depending on species *(14)*, are released and wind disseminated. Germination of the seeds is epigeal and good on moist, bare soil.

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Seeds may be extracted readily from air-dried fruits. Cleaned seed yields range from 661,000 to 1,653,000/kg (300,000 to 750,000/lb) depending on species and location *(13)*. Germination of seeds stored for 2 years under conditions ranging from 6 to 16 percent moisture content and −7° to 3° C (20° to 38° F) can be from 40 to 50 percent *(7)*. No pregermination treatment is required *(13)*. Broadcast sowing of seeds followed by a thin topping of soil or other nursery medium sufficient to give 215 to 323 seedlings/m² (20 to 30/ft²), can result in outplantable seedlings within 3 months.

Seedling development is partly dependent on the presence of a symbiont, the filamentous actinomycete *Frankia* spp., which allows casuarina to fix atmospheric nitrogen. Inoculation of nursery-grown seedlings is therefore advisable. This can be accomplished by application of a 10 percent suspension of ground casuarina root nodules with water to the nursery medium *(11, 18)*.

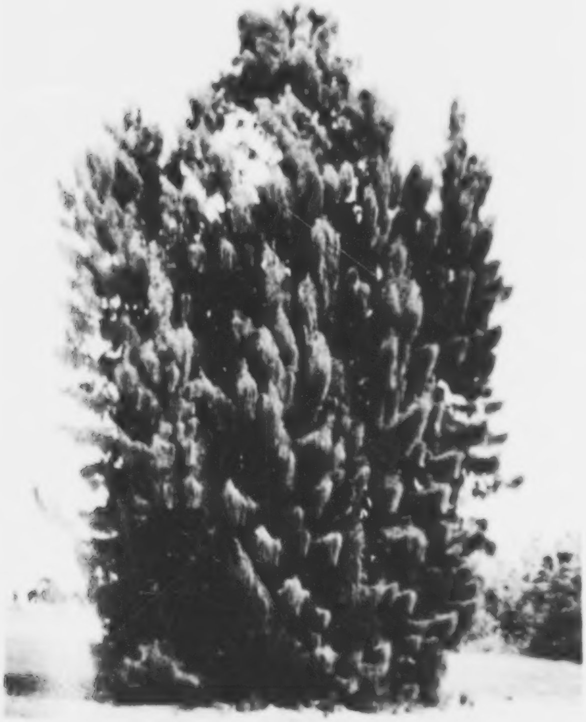

Figure 1.—A Casuarina glauca *specimen near Miami, FL, that shows prolific root suckering. (Courtesy D. L. Rockwood, University of Florida.)*

Seedling Development—Under proper conditions, growth of casuarina seedlings is extremely rapid, with growth rates of more than 2 m (6.5 ft) possible the first year. Such rates of growth are observed only when no competing herbaceous vegetation is present and may be possible only when the seedlings have been inoculated with *Frankia* spp., as noted earlier *(11)*.

Vegetative Reproduction—The three species show different levels of root suckering: *C. glauca* root suckers prolifically (fig. 1); *C. cunninghamiana*, infrequently; and *C. equisetifolia*, not at all. Rooting success, as evidenced by preliminary trials with fine branches from lower to middle portions of crowns, is satisfactory for *C. cunninghamiana* and *C. glauca* but low for *C. equisetifolia*. Use of rootone and a sand medium typically resulted in rooting as high as 50 percent in the spring. Grafting appears to be successful *(1)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Early growth is rapid, and height increments exceeding 1.5 m (5 ft) per year are common. Mature trees in stands of *C. cunninghamiana* and *C. equisetifolia* may reach 32 m (105 ft) in height and 41 cm (16 in) in d.b.h.; more commonly, heights of 25 m (82 ft) and diameters of 25 cm (10 in) are attained. Initial survival rates for planted trees are acceptable, averaging over 87 percent. One 35-year-old stand of *C. glauca* had a basal area of 90 m²/ha (392 ft²/acre) composed of trees averaging 19 m (62 ft) in height and 14 cm (5.5 in) in d.b.h.

Total aboveground dry biomass yields of young natural stands of *C. equisetifolia* have been as high as 16.6 t/ha (7.4 tons/acre) per year. Such stands, with densities up to 11,400 trees per hectare (4,600/acre), have trees ranging from 0.6 to 18 cm (0.25 to 7 in) in d.b.h., with an average of 4.3 cm (1.7 in) at an estimated age of 7.5 years.

Rooting Habit—Casuarina has a spreading, fibrous root system that can penetrate quite deeply into the soil if subsurface moisture is available. A very dense mat of adventitious roots may be formed in response to wet conditions. The root hairs become infected by *Frankia* spp. and form nitrogen-fixing nodules *(18)*.

Reaction to Competition—*Casuarina* species are intolerant of shade but capable of rapidly invading new sites and forming pure stands. When young, trees are easily suppressed by some forms of competing vegetation, especially grasses and sedges, particularly if seedlings are not nodulated and cannot fix atmospheric nitrogen. On a well-prepared palmetto prairie in Florida, for example, newly planted casuarina seedlings failed to survive competition from wiregrass (*Aristida stricta*) that rapidly reinvaded the site. In the Philippines and in the Highlands of Papua, New Guinea, however, casuarina seedlings have been reported to compete aggressively against *Imperata* grass, a weed that makes large areas of the tropics useless for agriculture (*12*). Once casuarina trees dominate a site, however, their heavy root mat and the deep litter layer tend to reduce, even eliminate, competitors.

Damaging Agents—Casuarina appears to have relatively few insect problems. The twig girdler (*Oncideres cingulata*) is harmful only to small trees; damage by the leaf notcher weevil (*Artipus floridanus*) usually is inconsequential; and one species of spittlebug (*Clastoptera undulata*) appears to infest individual trees but causes no serious damage (*2*). The Australian pine borer (*Chrysobothris tranquebarica*) has on occasion devastated trees 5 years or less in age by girdling the stems (*17*).

The major biological cause of death of casuarina on well-drained, acid, sandy soils is a mushroom root rot (*Clitocybe tabescens*) (*15*); *Casuarina cunninghamiana* may be less susceptible than the other species. The incidence of root rot is reduced on wetter sites, with no evidence of the disease in alkaline soils.

Primary nonbiological losses are from lightning and frost. Killing lightning strikes are common to casuarina that are dominant in the south Florida landscape. Freezing temperatures can damage well-established trees; temperatures of approximately −8° C (18° F) kill trees less than 0.5 m (1.6 ft) in height.

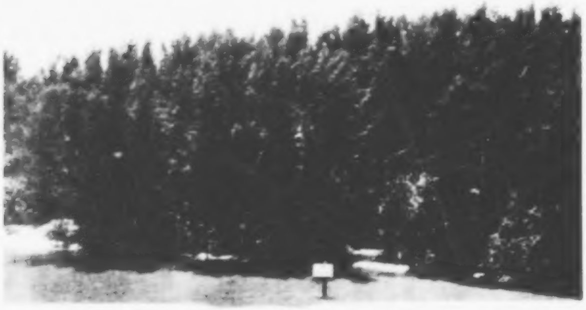

Figure 2—*Dense 7.5-year-old stand of* Casuarina equisetifolia *near Indian Rocks Beach, FL. (Courtesy L. F. Conde, University of Florida)*

Special Uses

No commercial use is made of casuarina in Florida, although its pulping properties are acceptable (*5*) and reputed to be better than those of eucalyptus (*Eucalyptus* spp.) (*8*). The species have been widely used for shelterbelts and in landscaping as hedges and ornamentals (*1*); *C. glauca* has been frequently planted for soil stabilization near drainage ditches and lakeshores (fig. 2).

The species are well suited for fuelwood because of their fast growth rates, coppicing potential and desirable wood properties. Their wood densities of approximately 0.72 are among the highest for Florida trees, their green wood moisture content is relatively low at 60 to 88 percent on an oven-dry basis, and their whole-tree energy values are considerably higher than those of other species (*16*). The ash content is slightly higher than that of most native American woods, averaging about 2 percent; the ash content of bark is twice this amount. The wood dries rapidly and burns well. Attempts to saw and season casuarina for use as lumber have not been satisfactory (*10*). Casuarina bark has been used in tanning and medicine, and the fruits have been used for novelties and decorations (*13*).

Genetics

The geographic seed origins of casuarina in Florida are not known. Although trees characteristic of each species can be readily located, classification of individual trees is sometimes difficult because a high degree of hybridization is presumed. The three species are found together in much of south Florida and have compatible flowering times. A *C. cunninghamiana* × *C. glauca* hybrid has grown faster than any of the three species (*1*). Studies of individual tree collections of *C. cunninghamiana* and *C. equisetifolia* from four areas in south Florida do not indicate differences among trees, sources, or species for survival through 6 months (*16*).

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Cecropia peltata L. Yagrumo Hembra, Trumpet-Tree

Moraceae Mulberry family

Susan R. Silander and Ariel E. Lugo

Yagrumo hembra (*Cecropia peltata*), also called trumpet-tree, is a rapidly growing neotropical tree, an important secondary species that is common in Puerto Rico. It is an early invader of forested areas subject to natural or human disturbances and is conspicuous due to its spreading crown and large peltate leaves 30 to 50 cm (12 to 20 in) in diameter, with silver-white lower surfaces.

Habitat

Native Range

Yagrumo hembra (fig. 1) is also native throughout the Greater and Lesser Antilles and in Central America from Yucatan, Mexico, to Costa Rica. In South America it has been reported from Venezuela, Colombia, Brazil, and the Guianas *(19)*.

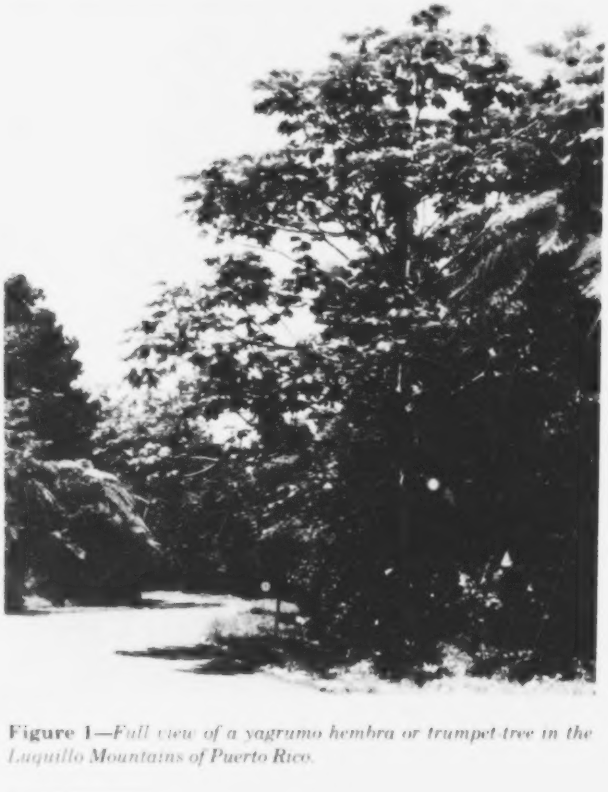

Figure 1—*Full view of a yagrumo hembra or trumpet-tree in the Luquillo Mountains of Puerto Rico.*

Climate

In Puerto Rico, yagrumo hembra is found most frequently in the wetter life zones: Subtropical Moist Forest, with 990 to 2010 mm (39 to 79 in) of precipitation annually; Subtropical Wet Forest, with 2010 to 3990 mm (79 to 157 in); Subtropical Rain Forest, with 3810 mm (150 in) and greater; Subtropical Lower Montane Rain Forest, with 2010 to 3990 mm (79 to 157 in); and Subtropical Lower Montane Wet Forest, with 3810 mm (150 in) and greater. Mean annual temperatures in the lower montane life zones range from 12° to 18° C (54° to 64° F), whereas in the lower elevation life zones the range is from 18° to 24° C (64° to 75° F). The species is rare or absent in the Subtropical Dry Forest life zone.

Soils and Topography

Yagrumo hembra grows on the Ultisols of the central and eastern mountains of Puerto Rico, the Mollisols and Alfisols of the limestone hills of the northwest, the Oxisols of the western mountains underlain by serpentine, and also the Mollisols and Inceptisols of the northern coastal plain. It is found from 50 to 1300 m (164 to 4,265 ft) in elevation on ridges, slopes, and flats but appears to be at its optimum in coves or protected areas. It is often found on steep slopes where landslides or tree falls have occurred, and in these areas its prop or stilt roots may be conspicuous. Yagrumo hembra grows on alluvial, colluvial, and residual soils neutral to acidic in nature. These soils may be derived from tuffs; volcanic rock, andesitic or dioritic in composition; limestone; or serpentine. Soil texture may range from heavy clay to sandy, but a clay-loam soil is optimal.

Associated Forest Cover

As a secondary species, yagrumo hembra frequently invades forest gaps or openings, roadsides, streamsides, and landslides in moist, wet, and rain forest life zones of Puerto Rico. In the Luquillo Mountains in eastern Puerto Rico and in the central mountains it is widely distributed in the Lower Montane Forest, Montane Rain Forest, and Elfin Woodland forma-

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tions of these life zones *(1)*. In the Elfin Woodland it is short in stature and gnarled, as are its associated species in this formation.

Yagrumo hembra is frequently associated with other secondary species such as yagrumo macho *(Didymopanax morototoni)* and guano *(Ochroma pyramidale)*. The scattered presence of this secondary species among species more characteristic of a mature stand indicates that a disturbance, such as tree fall, storm damage, or landslide, occurred at some time in the past. Although initially dependent upon the size of the openings, pure dense stands of yagrumo hembra, once established, may persist for several years following the disturbance. The species may also be found, in a dominant or codominant canopy position, associated with primary species such as tabonuco *(Dacryodes excelsa)*, motillo *(Sloanea berteriana)*, and ausubo *(Manilkara bidentata)* in the Lower Montane Rain Forest; palo colorado *(Cyrilla racemiflora)*, caimitillo *(Micropholis chrysophylloides)*, and camasey jusillo *(Calycogonium squamulosum)* in the Montane Rain Forest; and roble de sierra *(Tabebuia rigida)* and nemoca *(Ocotea spathulata)* in the Elfin Woodland.

Yagrumo hembra is less common in the hotter lowlands of Puerto Rico. Here it may be an infrequent component of succession primarily on the wetter sites following cultivation, associated with the secondary species listed above as well as with many introduced species. In the mogotes or limestone hills of northwestern Puerto Rico, yagrumo hembra is associated with those secondary species described previously as well as others such as ucar *(Bucida buceras)*, almacigo *(Bursera simaruba)*, and espino rubial *(Zanthoxylum martinicense)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yagrumo hembra is dioecious, with staminate flowers borne in slender, stalked aments 5 to 6 cm (2.0 to 2.4 in) in length, arranged in clusters of as many as 15, and pistillate flowers in thicker, stalkless aments grouped in clusters of only 2 to 5. Both staminate and pistillate trees may be observed in flower and fruit all year long. However, a peak flowering and fruiting period occurs in Puerto Rico during the months of January to March, the drier season. This is also the period of minimum temperatures and minimum day-length *(8,26)*. A winter flowering and fruiting peak for yagrumo hembra has also been noted in San Pedro de Montes de Oca (1200 m or 3,937 ft) in Costa Rica *(9)*.

The slightly fleshy multiple fruit is at maturity gray-green in color and may be 10 cm (4 in) in length and 15 mm (0.6 in) in diameter. It is composed of numerous individual fruits, pentangular or hexangular in shape, each of which contains one brown seed of about 2 mm (0.08 in) in length. There are 2,500 seeds per gram (70,875/oz), air dried. The extraction factor for seeds is about 20 percent, because of the gummy material surrounding each seed *(16)*. Maturation, from emergence of the inflorescence from the terminal bud to full ripening, requires from 3.5 to 4 months. Staminate inflorescences remain on the tree for only 1.5 months and produce copious amounts of wind-borne pollen approximately 1 to 1.5 months following emergence from the terminal bud *(26)*.

Seed Production and Dissemination—Although as many as 15,000 flowers may be produced per inflorescence, the number of seeds that mature fully may be as low as 18 percent, or 2,725 viable seeds per inflorescence. Seed production by a mature tree during one reproductive year has been estimated to be as high as 1 million *(13,26)*. Seed production is size or age specific, however, and increases throughout the lifetime of the tree. In an estimated life span of 30 years, as many as 6 to 7 million seeds may be produced by a single tree. Reproductive maturity is reached at an earlier age, 3 or 4 years by pistillate than by staminate trees, which mature at 4 to 5 years. Reproductive age may depend upon need for allocation of resources to rapid initial height growth and therefore the height and proximity to surrounding vegetation. Roadside trees, in a more open environment, reached reproductive maturity sooner (3 to 4 years) than forest gap trees (5 to 6 years) *(26)*. Seed production probably decreases as a tree approaches the senescent state. In this stage there appears to be an increase in branch loss.

Seeds are dispersed primarily by bats and birds *(3,7,11,18,24)*; seeds pass through the digestive tracts unharmed *(24)*. In Puerto Rico, 15 species of birds and bats have been reported to feed on mature yagrumo hembra fruit. Some of the more common species include the Jamaican fruit eating bat, the banana quit, the pearly-eyed thrasher, the red-legged thrush, and the reina mora *(18,26)*.

These species frequent both open and forested areas, so that seeds are dispersed widely and are available in forest soil in the event of a disturbance *(12)*. As many as 398 seeds per square meter (37/ft^2) have been reported to be present in undisturbed lower montane rain forest soil *(2,26)*. Blum *(3)* reported that yagrumo hembra seedlings grew in 4 to 10 soil samples taken from mature forests in

Panama. Other secondary species such as yagrumo macho, cachimbo comun (*Psychotria berteriana*), and guano were also present in these soils.

Seeds may also be dispersed when the entire fruit cluster falls to the ground upon ripening, but these seeds show a reduced viability as the embryos are damaged by fungi and insects of the family Nitidulidae. Laboratory-stored seeds retained viability for a minimum of 6 months, whereas seeds stored on the forest floor retained viability for only 2 to 3 months. This reduced viability under natural conditions indicates that a constant addition of seeds to the seed bank of the forest floor is necessary for rapid and successful colonization of a forest gap.

Seedling Development—Seeds require full sunlight for successful germination. Thus, seeds present on the floor of closed forests germinate only when some type of canopy gap occurs. Given full light conditions, germination may be as high as 80 to 90 percent *(3,16,26)*. Germination is epigeal and in an open field was shown to be reduced by the presence of a layer of leaf litter. Other factors that may interact with increased light intensity in promoting germination include higher surface soil temperatures, fluctuations in air temperature, and changes in soil moisture. With the decreased light intensity beneath the closed forest canopy, spectral composition (an increased proportion of infrared light) may also become critical to germination *(26)*. A decreased ratio of infrared to red light has been shown to inhibit germination of successional species. In open fields there was less yagrumo hembra seed germination than was observed in light gaps. This may result from the extremely high and fluctuating surface soil temperatures or to fluctuating but frequently low soil moisture, or both (table 1).

Table 1—Microclimatic– and physical factors of selected environments *(26)*

Item	Environment[1]		
	Open field	Forest	Gap[2]
Temperature, °C			
Mean	25.4	22.7	23.2
Daily variation	8.4	2.4	3.0
Soil surface	30.2	22.3	24.8
Temperature, °F			
Mean	77.7	72.9	73.8
Daily variation	47.1	36.3	37.4
Soil surface	86.4	72.1	76.6
Relative humidity, percent			
Mean	77	94	85
Daily variation	34.0	4.5	10.3
Soil moisture, % dry wt.	47.8	78.3	47.6

[1] Values are means for all months, August 1977 to January 1978 (25).

In the nursery, seed is germinated under light shade on a seedbed prepared from equal parts of clay, sand, and filter press cake. Light shade is maintained until seedlings shade the germination media *(16)*.

Seedling leaves are distinct from those of the mature plant. They are downy on both surfaces, lanceolate, unlobed, and finely toothed. In the early sapling stage, 0.5 m (1.6 ft) tall, leaves begin to show signs of lobing. Ultimately, new leaves have 7 to 11 palmate lobes and resemble those of the mature plant, dark green and scabrous above and covered with a dense surface of white hairs below. Seedlings grow rapidly in height, reaching 10.0 to 15.0 cm (3.9 to 5.9 in) in 10 weeks *(16)* and as much as 2.1 m (6.9 ft) in the first year *(21)*. The ratio of photosynthesis to respiration of yagrumo hembra seedlings has been reported to be much greater than 1 *(20)*.

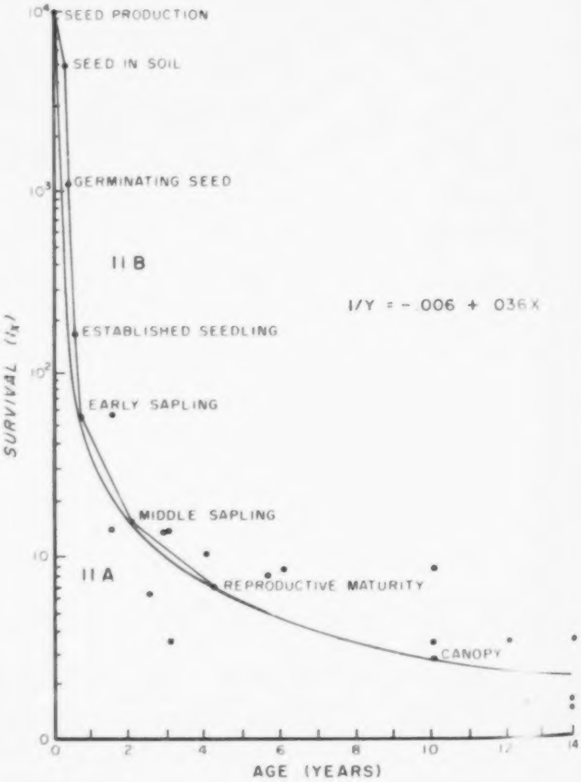

Figure 2—*Survivorship curve for yagrumo hembra. A is based on disturbed areas; B is based on life cycle stages* (26).

Under natural conditions, seedling mortality may be extremely high. In a forest opening, 99 percent of germinating seedlings may die within the first year (fig. 2). This is the life stage during which the greatest mortality occurs. During nursery trials, volunteer seedlings suffered 45 percent mortality during the first 9 months *(10)*. However, seedlings transplanted when 25.0 to 60.0 cm (9.8 to 23.6 in) in height to the field following a 2-week shaded period and gradual diminishing of shade showed a survival of as high as 80 percent. In 7 months they had reached 2.0 m (6.6 ft) in height *(16)*.

Growth in height is most rapid during the first 4 to 5 years, but the tree grows relatively little in diameter during the same period *(6)*. In the Luquillo Mountains of eastern Puerto Rico, maximum seedling height growth under natural conditions was 1.14 m (3.7 ft) and the mean 0.73 m (2.4 ft) per year. Maximum diameter growth measured immediately above the root collar was 5 mm (0.20 in) and the mean growth was 3.6 mm (0.14 in) during an 8-month period *(26)*.

Seedlings which are overtopped and thus shaded for extended periods of time do not survive for long. Potted seedlings transferred from a forest gap to closed forest died within several months and showed little if any growth. Potted seedlings remaining in the gap exhibited 100 percent survival as well as diameter and height increases. A disturbed area that is invaded rapidly by grasses, ferns, or vines shows a decreased density of yagrumo hembra during the seedling and sapling stages *(26)*.

Vegetative Reproduction—Yagrumo hembra sprouts easily.

Sapling and Pole Stages to Maturity

Growth and Yield—The sapling life stage begins when lobing of new leaves increases. Diameter growth of nonsuppressed saplings is significantly faster than that of seedlings. At an elevation of 400 m (1,312 ft) in the eastern mountains of Puerto Rico, saplings grow a maximum of 3.0 cm (1.2 in) and a mean of 6.5 mm (0.26 in) in diameter per year. Mean growth in d.b.h., as opposed to maximum d.b.h. growth, is low due to the presence of numerous suppressed saplings in the dense stands which often occur following disturbance. These saplings grow as much as 2.16 m (7.1 ft) in height per year *(26)*.

A method has been developed for determining the age of yagrumo hembra based on past height growth *(6)*. The tree has conspicuous rings and large triangular leaf scars at each node. Turrialba, where the study was conducted, has a distinct dry season, and internodes are arranged in short and long series. Short internodes represent growth during the drier season and long internodes growth during the wetter season. Annual height growth was found to be faster in wetter (5.9 m or 19.3 ft and 7.6 m or 24.9 ft) than in drier (1.9 m or 6.2 ft and 2.4 m or 7.9 ft) regions. It should be stressed that this method is only reliable for trees less than 5 years in age as height growth slows significantly later in life *(6)*. Another method for aging yagrumo hembra is based on regressions of height and diameter on age (fig. 3). Since this method was developed for young trees and uses mean d.b.h. and mean height of a stand, it may more accurately estimate stand than individual age *(26)*.

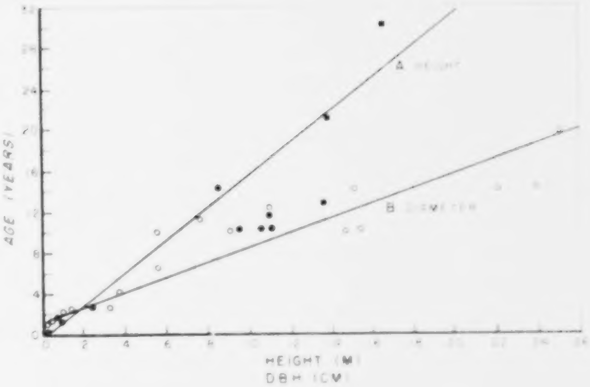

Figure 3—*Estimation of age of yagrumo hembra from diameter and height*

A = *regression of age of disturbed area on mean height (solid dot)*. *Y* = *0.91* + 1.3X, r^2 = *0.8*. *B* = *regression of age of disturbed area on mean d.b.h. (open dot)*. *Y* = *0.90* + 0.86X, r^2 = *0.9 (26)*.

Periodic diameter growth of 4.6 to 5.1 mm (0.18 and 0.20 in) was measured for yagrumo hembra *(5)*. Growth rates were among the slowest measured in the Luquillo Mountains. A mean annual growth rate in d.b.h. of 2.0 mm (0.08 in) has been reported for mature yagrumo hembra trees *(23)* and an annual diameter growth rate of 6.4 mm (0.25 in) was measured in mature dominant trees *(26)*. Once yagrumo hembra trees reach maturity, diameter growth appears to decrease. Growth is greatly improved by a dominant crown position, but little difference is found among codominant, intermediate, and suppressed trees. Trees in plantations reach a diameter of 25.0 cm (9.8 in) and a height of 14.0 m (45.9 ft) in 21 years *(25)*. Height growth in yagrumo hembra predominates over diameter growth *(23)*. This pattern fits well the ecological role of yagrumo hembra as a gap species.

In the Luquillo Mountains, the density of yagrumo hembra in the tabonuco forest association (Subtropical Wet) is 83 trees per hectare (34/acre), and at a higher elevation in the Colorado forest association (Lower Montane Wet) it is 17 trees/ha (7 trees/acre) *(28)*. Yagrumo hembra had a mean basal area of 18.3 to 22.9 m^2/ha (79.7 to 99.7 ft^2/acre) in the tabonuco forest *(16)*. In a 2-ha (4.9-acre) sample of tabonuco forest, approximately 25 percent of the trees were 10 to 15 cm (3.9 to 5.9 in) in d.b.h, 26 percent were 15 to 20 cm (5.9 to 7.9 in), 20 percent were 20 to 25 cm (7.9 to 9.8 in), and 13 percent were 25 to 30 cm (9.8 to 11.8 in). Only 6 percent had diameters of greater than 50 cm (19.7 in).

Trees reach canopy height at about 10 years of age and thereafter survive in the canopy for approximately 20 years. Mean further life expectancy, 10.25 years, is greatest as the tree approaches the canopy. High mortality occurs between the production of seed and the establishment of seedlings (fig. 2).

Rooting Habit—The root system of yagrumo hembra tends to be superficial, and therefore the tree is easily uprooted, particularly when immature. Prop or stilt roots are a prominent feature and are often as much as 1.0 m (3.3 ft) in height.

Reaction to Competition—Yagrumo hembra is most accurately classed as intolerant of shade. This is especially true during the seedling and sapling stages. Competition for light and space during these stages may be the principal factor influencing growth and survival.

Damaging Agents—In the seedling and sapling stages a major cause of mortality is defoliation by the larvae of the following: *Prepodes* spp., *Gynaecia dirce*, *Historis odious*, *Correbidia terminalis*, and *Sylepta salicalis (22)*. The cotton or melon aphid (*Aphis gossypii*) is also commonly observed on leaves of yagrumo hembra.

The above species often cause heavy damage to the leaves of mature trees. Strangulation by vines, including those of the families Leguminosae, Convolvulaceae, and Malpighiaceae *(27)*, as well as many species of *Philodendron*, is also a major cause of mortality, particularly during the sapling stage. Mortality of mature trees may be caused by storm damage to the easily broken branches, by advancing age, or by environmental changes, such as shading and root competition, caused by the reestablishment of the climax forest.

Special Uses

As a dominant secondary species, yagrumo hembra is invaluable in regeneration of the forest following disturbance. As it rapidly forms a dense stand, nutrients may be conserved and the environment beneath ameliorated sufficiently to allow species characteristic of a later stage of succession to germinate and grow. In this manner the soil may be stabilized following a disturbance such as a landslide. Its broad canopy protects the soil from excessive erosion and reestablishes shade conditions to the forest floor.

With a specific gravity of 0.29, the wood of yagrumo hembra is only slightly heavier than local balsa. The wood is used in the finish of "puertorican cuatros," a local guitarlike musical instrument. Principal uses for wood in Puerto Rico once included excelsior. The wood also was shredded and mixed with cement to form a building or insulation board *(4)*. Elsewhere, yagrumo hembra is used to produce paper pulp. Fiber yield per cord of fresh material is low, but it cooks rapidly, giving unbleached pulps that approach the best northern deciduous neutral sulfite pulps, e.g., aspen, in quality. A yield of 56 kg (123.5 lb) of pulp per 100 kg (220.5 lb) of wood has been estimated *(17)*. The wood may be substituted for use in products made from heavier grades of balsa. It is also used for boxes, crates, and matchsticks *(19)*. The hollow branches are often split and used for gutters or troughs, and entire branches are used for pipe floats, life preservers, and tamborines.

Various substances have been extracted from yagrumo hembra for medicinal use *(19)*, including one that increases cardiac muscular contraction and acts upon the kidneys as a diuretic. A substance extracted from the roots is said to heal wounds, and the leaves are often used as a poultice to reduce swelling and as an abrasive *(27)*.

Genetics

Vegetative morphology of yagrumo hembra throughout the islands of the Caribbean differs from that of mainland (Central and South America) representatives of the same species. On the mainland, yagrumo hembra maintains a symbiotic relationship with *Azteca* ants. The species *Azteca constrictor* and *A. alfaroi* have been reported from Venezuela *(27)*. There the tree also has adaptations, such as a trichilium or highly modified petiole bases that produce mullerian bodies or food bodies rich in glycogen. The stinging, aggressive ants live in the hollow internodes and feed upon glycogen produced by the tree. Neither the adaptations nor the ants are present on trees in Puerto Rico. In the Caribbean islands from Trinidad to Puerto Rico there is a progressive loss of these ant-related traits *(25)*. Mainland individuals maintain trichilia in the greenhouse. These appear to be genetic traits and do not depend on ant stimulation for development *(14,25)*.

Approximately 80 species of the genus *Cecropia* have been described; however, only one species is found in the islands of the Caribbean. A chromosome number of 2n=28 has been reported *(27)*. Velazquez *(27)* consolidated three Venezuelan *Cecropia* species into a variety of *C. peltata*: *Cecropia peltata* L. var. *candida*.

Recently, Howard *(14)* describes Puerto Rican species as *Cecropia schreberiana* rather than *C. peltata*, stating that the latter is restricted to mainland Central and South America and Jamaica. *C. schreberiana* is mentioned as occurring throughout the remainder of the Greater and Lesser Antilles. Some place it in its own family, cecropiaceae, with the genus *Cecropia* as the type genus.

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Cedrela odorata L. Cedro Hembra, Spanish-Cedar

Meliaceae Mahogany family

Barbara B. Cintron

Cedro hembra (*Cedrela odorata*) is the most commercially important and widely distributed species in the genus *Cedrela*. Known as Spanish-cedar in English commerce, the aromatic wood is in high demand in the American tropics because it is naturally termite- and rot-resistant. Cedro is widespread but never very common throughout moist tropical American forests; its numbers are continuing to be reduced by exploitation without successful regeneration. An understanding of the exacting site requirements and of associated damage by insects is needed for productive plantations.

Habitat

Native Range

Cedro is a tree of the New World tropics, appearing in forests of moist and seasonally dry Subtropical or Tropical life zones *(24)* from latitude 26° N. on the Pacific coast of Mexico, throughout Central America and the West Indies, to the lowlands and foothills of most of South America up to 1200 m (about 4,000 ft) altitude, finding its southern limit at about latitude 28° S. in Argentina *(12,55)*. Cedro is always found naturally on well-drained soils, often but not exclusively on limestone; it tolerates a long dry season but does not flourish in areas of rainfall greater than about 3000 mm (120 in) or on sites with heavy or waterlogged soils *(5,34,40,66)*. Individual trees are generally scattered in mixed semievergreen or semideciduous forests dominated by other species *(11,23,25,28)* (fig. 1).

Climate

Cedro is a climatic generalist, found over a wide geographic range of warm latitudinal belts, from Subtropical Dry Forest (wet transitional part) in Mexico and parts of the West Indies, through Subtropical Moist Forest to Subtropical Wet Forest in the West Indies and Central America, to Tropical Moist and Wet and Tropical Premontane Moist and Wet life zones in the equatorial regions *(24)*. It is most abundant in the lowlands and foothills (other species, *C. montana* and *C. lilloi*, replace it at higher elevations) in moist forests. Its distribution is within the frost-free tropics for the most part, although it has been collected at latitudes 26° N. and 28° S., where occasional light frosts can be expected *(2,55)*. Mean temperatures of 23° to 26° C (73° to 79° F) are found in the Caribbean part of its range; in tropical South America mean temperature is slightly higher, 28° C (82° F), with a mean minimum of 23° C (73° F) and a mean maximum of 32° C (90° F). At the southern limit of its range in Argentina the mean temperature is 24° C (75° F); mean maximum temperature is 30° C (86° F) and mean minimum is 18° C (64° F) *(16,34,60)*.

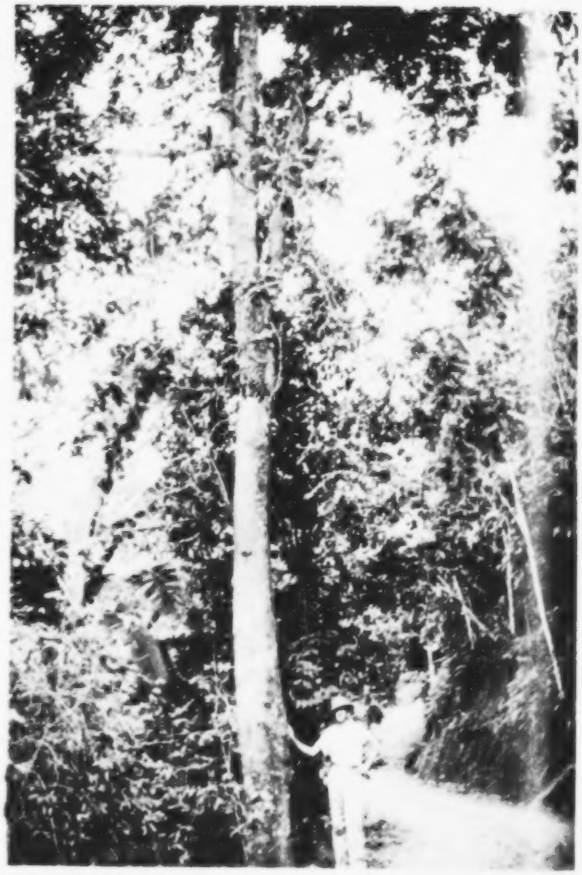

Figure 1—*Cedro hembra in a mixed forest.*

Cedro develops best in seasonally dry climates, as reflected in its deciduous habit and its formation of

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(presumably annual) growth rings. It reaches greatest prominence under an annual rainfall of 1200 to 2400 mm (47.2 to 94.5 in) with a dry season 2 to 5 months long. Both tree growth and reproduction are synchronous with the onset of the rains *(40,5[illegible]*. Cedro survives in lower rainfall areas (down to about 1000 mm (40 in) annually) but grows slowly and shows a stunted form *(41,59)*. It also grows sporadically in areas receiving up to 3500 mm (138 in) of rainfall, but only on very well-drained sites *(23,5[illegible]*. In Central and South America, in areas with less than 2000 mm (about 80 in) annual rainfall and over limestone-derived soils, cedar may become locally the dominant species *(34,57)*.

Soils and Topography

Cedro may be exacting in its soil requirements but these are still imperfectly understood. In the West Indies it is most commonly found on limestone-derived clay soils *(23,35,47)*, but it also grows on well-drained sites over acid soils derived from volcanic rock (Ultisols). The common denominator appears to be drainage and aeration of the soil *(24,52,63)*, not soil pH *(40,64,65)*. In Trinidad the one factor common to all sites supporting good growth was good surface drainage *(10,40)*. In Mexico and Central America, cedro is likewise common on well-drained soils and ruins *(48)*. Soil fertility may also be important, as in some tests cedro grew better in soil enriched with the burned remains of secondary forest *(10,58)*. No definitive studies of nutrient requirements beyond the seedling stage have been performed *(5,63)*. Symptoms of stress due to poor soils are burned appearance of roots, development of "weeping willow" form in saplings (leaves become thin and drooping) or loss of leaves at irregular intervals during the wet season.

Associated Forest Cover

In Puerto Rico, cedro is found in Subtropical Moist and Subtropical Wet life zones but is commonest in the Subtropical Moist life zone over limestone-derived soils *(16,35)*. Other species commonly found in the tree layer of this association in Puerto Rico are tortugo amarillo *(Sideroxylon foetidissimum)*, sanguinaria *(Dipholis salicifolia)*, moca *(Andira inermis)*, aquilon *(Terebraria resinosa)*, ucar *(Bucida buceras)*, cupey *(Clusia rosea)*, guano *(Ochroma pyramidale)*, maga *(Montezuma speciosissima)*, uvilla *(Coccoloba diversifolia)*, espino rubial *(Zanthoxylum martinicense)*, almacigo *(Bursera simaruba)*, and cedro macho *(Hyeronima clusioides)*. Almost all of these species have a much wider local distribution and greater abundance than cedro itself, however. In the continental part of its range, cedro is often associated with mahogany *(Swietenia* spp.) in moist and wet forests, but mahogany is usually present in far greater abundance *(52)*. Compared to the closely related mahoganies, cedro is much more exacting in site requirements, especially drainage. Near the high rainfall end of its climatic range, cedro is invariably found on ridgetops, upper slopes, old building ruins, and road banks, or other areas of unusually well aerated soil *(23)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Cedro's reproductive cycle is synchronized with the growing season of the site; throughout its range it flowers at the beginning of the rainy season: May to August in Mexico, the West Indies, and northern South America *(4,30,48)*; September to October in Argentina *(34)*. Flowering begins when new leaves are expanding. The large and much-branched inflorescences bear numerous small, five-part, symmetrical greenish-white flowers. Trees are monoecious; male and female flowers are borne on the same inflorescence but the species is proterogynous (female flowers open first). Fruit development takes about 9 or 10 months and fruits ripen during the next dry season. Trees begin to fruit at an age of 10 to 12 years. The fruit, a large woody capsule, is borne near branch tips. Fruits ripen, split, and shed seeds while still attached to the parent tree.

Seed Production and Dissemination—Fruits open from the top downward to release 40 to 50 winged seeds when ripe. Seed weight is about 8 to 10 percent of dry fruit weight. One kilogram (2.2 lb) contains 20,000 to 50,000 seeds (9,100 to 22,700/lb, approximately). Seeds are 20 to 25 mm (0.75 to 1.0 in) long, wing included, and are wind dispersed. Heavy seed crops are produced annually in some areas and biennially or irregularly in others *(41,59)*. Seeds are shed during the dry season. They lose viability quickly if not stored very dry at reduced temperatures *(12,37,38)*. Germination begins with the onset of the rainy season and is epigeous. Vigorous germination is the rule, with seed viability reportedly up to 90 percent *(40)*. No seed dormancy period is known. Germination is rapid, usually completed within 2 to 4 weeks *(37,38)*.

Seedling Development—Early development of the seedling is rapid as long as moisture and light are adequate *(5,46,62)*. Shade-grown seedlings saturate photosynthetically at low intensities and are shade tolerant, but sun-grown seedlings require high light intensities for best growth *(27,28,29)*. Shade-grown seedlings are susceptible to sunscald and subsequent insect attack when moved to sun *(43)*. Fertilizer trials showed best growth with 7-6-19 fertilizer *(6)*.

In natural forest, high seedling densities are common near fruiting trees shortly after the beginning of the rainy season, but most of these seedlings disappear by the middle of the rains or a little later; this high natural mortality may be due to shade or competition but is thought to be partly due to damping off or other root problems *(40)*. Seedlings and saplings have extremely shallow root systems and are sensitive to uprooting and root trampling *(10)*. Seedlings average 1 m (3.3 ft) in growth and develop a stem diameter of 10 mm (0.4 in) or more during the first year under favorable conditions (table 1). Early growth is vigorous under partial shade, when the shootborer attack is not severe *(8,51,62)*.

Natural cedro regeneration from seed is good in many parts of Central and South America, but good initial growth is often followed by dieback after 2 to 3 years. This problem may be only partially related to the shootborer and may also reflect the scarcity of appropriate soils, especially in some of the areas subjected to most intensive study. The abundance of cedro regrowth as almost pure stands with no apparent shootborer problems on recent and ancient limestone ruins in areas with a strong dry season *(52)* suggests that cedro may be a calciphile.

In some parts of the neotropics selective removal of seed trees has left the forest with insufficient stock for natural regeneration, even on favorable sites. Some success has been claimed for artifical regeneration using the taungya method (a system using native farmers who plant the trees interspersed with their food crops, abandoning the field later to return to forest, now enriched with the desired plantation species); line plantings followed by natural liberation are also used *(11,42,58)*. Successful establishment by the taungya system has been achieved in Africa, where extensive areas of well-drained soils are present, and the native shootborer does not attack New World cedro *(34)*.

Vegetative Reproduction—Cedro does not coppice readily nor produce root suckers; it is not fire resistant *(5,40)*. It is capable of pollard regrowth (partial terminal regrowth after moderate wind damage or partial dieback) if the tree is well established. It can be grafted and air-layered *(34,40,56)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth data for many plantations are summarized in table 2. Once past the vulnerable early sapling stage, cedro is a very fast-growing tree, adding 2.5 cm (1.0 in) or more in diameter and 2 m (6.6 ft) in height a year under good conditions. Provenance differences in height growth show up most clearly in Africa, where shootborer attacks are not a problem *(44)*. Fast-growing saplings develop straight, clean boles and narrow, thin crowns. The light-demanding saplings escape shootborer attack in 3 to 4 years if robust, and subsequent growth is rapid on favorable sites *(58)*. The smooth, grayish bark of the sapling gradually becomes vertically fissured as the tree matures, and turns somewhat brownish. Large cedros have a straight, clean bole, often 15 to 20 m (49 to 66 ft) to the first limb and a narrowly buttressed base. Maximum height is 30 to 40 m (98 to 131 ft) *(34)*.

Table 1—Early seedling growth of cedro hembra *(Cedrela odorata)*

Country	Origin of test material	Germination	Annual growth[1]				Survival
			Height		D.b.h.		
		pct	*cm*	*in*	*cm*	*in*	*pct*
Puerto Rico *(62)*							
Full sun	5 Provenances	10 to 62	26.2	10.3	8.4	3.3	98 to 100
St. Croix, VI *(62)*							
Shade	5 Provenances	nr[2]	29.3	11.5	8.5	3.3	93 to 97
Venezuela *(4)*	Venezuela	85 to 90	120	47.2	nr	nr	[illegible]
Trinidad *(39)*	Trinidad	90	100	39.4	nr	nr	[illegible]
Nigeria *(14,44)*	15 Provenances	nr	133.7	52.6	34.8	13.7	[illegible]
Uganda *(30)*	12 Provenances	"good"	141.0	55.5	23.5	9.3	75 to 96
Tanzania *(48)*	5 Provenances	nr	95	37.4	nr	nr	[illegible]

[1] All growth data were converted to an annual basis.
[2] Not reported.

Table 2—Growth of cedro hembra (*Cedrela odorata*) in plantations

	Plantation site			Plantation				Annual growth
Location	Rainfall	Soil	Origin of seed	Age	Spacing	D.b.h.	Height	in d.b.h.
	mm			*yr*	*m*	*cm*	*m*	*mm*
Puerto Rico *(64,65)*	1900	limestone	6 Provenances	8	2.4	4.4	4.5	5.6
Virgin Is., USA *(64,65)*	1000 to 1200	shallow, over shale	5 Provenances	8	2.4	5.9	4.5	7.4
Ivory Coast *(13)*	1300 to 1500	granite-derived sandy loam	8 Provenances	7.5	nr[1]	18.2	13.7	24.3
Nigeria (Ore) *(14,15)*	1600	shallow sandy loam pH 5.5	11 Provenances	7.5	3.6	23.9	14.8	31.9
Tanzania *(6,50)*	1450	"well drained"	8 Provenances	5.6	4	16.1	12.5	28.8
Mexico *(59)*	1200	limestone-derived	Mexico "Mexicana"	8	0.5	12.0	10	15.0
Ecuador *(59)*	1200	alluvial, sandy	Cuba	6	2 by 4	24.0	18	40
Jamaica *(59)*	2500	limestone, light clay	Jamaica	5	2.5 (in lines)	8	nr	16
Mexico *(59)*	1100	limestone, thin stoney clay	Mexico	8	3	11	6	14
Mexico *(59)*	900	limestone, sandy clay	Mexico	12	1	8	6	6.7
Panama *(59)*	2600	alluvial, well drained	Panama	12	1.5 by 3	24	21	20
Honduras *(59)*	1800	limestone and volcanic	Honduras	13	1.5 by 3	28	15	21.5
Trinidad *(59)*	2400	limestone, well drained	Trinidad	15	nr	32	23	21.3
Ecuador *(59)*	1200	alluvial	Cuba	18 to 20	3	50	25	25.0
	in			*yr*	*ft*	*in*	*ft*	*in*
Puerto Rico	75	limestone	6 Provenances	8	8.0	1.7	14.8	0.22
Virgin Is., USA	39 to 47	shallow, over shale	5 Provenances	8	8.0	2.3	14.8	0.29
Ivory Coast	51 to 59	granite-derived sandy loam	8 Provenances	7.5	nr	7.2	44.9	0.96
Nigeria (Ore)	63	shallow sandy loam pH 5.5	11 Provenances	7.5	11.8	9.4	48.6	1.26
Tanzania	57	"well drained"	8 Provenances	5.6	13.1	6.3	41.0	1.13
Mexico	47	limestone-derived	Mexico "Mexicana"	8	1.6	4.7	32.8	0.59
Ecuador	47	alluvial, sandy	Cuba	6	6.6 by 13.1	9.4	59.0	1.57
Jamaica	98	limestone, light clay	Jamaica	5	8.2 (in lines)	3.1	nr	0.63
Mexico	43	limestone, thin stoney clay	Mexico	8	9.8	4.3	19.7	0.55
Mexico	35	limestone, sandy clay	Mexico	12	3.3	3.1	19.7	0.26
Panama	102	alluvial, well drained	Panama	12	4.5 by 10	9.4	68.9	0.79
Honduras	71	limestone and volcanic	Honduras	13	4.5 by 10	11.0	49.2	0.85
Trinidad	94	limestone, well drained	Trinidad	15	nr	12.6	75.5	0.84
Ecuador	47	alluvial	Cuba	18 to 20	9.8	19.7	82.0	0.98

[1] Not reported.

Natural forests containing cedro in Mexico yielded only 2000 m³ (about 71,000 ft³) per year in a total area of 160 000 ha (1,137,000 acres), for an annual yield of 0.004 m³/ha (0.057 ft³/acre). Mahogany yields from the same forest were eight times higher. This illustrates the present low stocking of cedro in natural forests, although the low density may be due in part to past exploitation and lack of regeneration *(52,53)*. In contrast, 40-year-old plantations in Africa yielded 455 m³/ha (6,500 ft³/acre) at the end of the rotation, and a yield of 150 to 270 m³/ha (about 2,100 to 3,800 ft³/acre) over a 35-year rotation was estimated for line-planted cedro in Surinam *(34,58)*. Webb et al. *(61)* cited 11 to 22 m³/ha (157 to 314 ft³/acre) per year for managed cedro plantations worldwide. Marshall calculated cedro yield by diameter classes in Trinidad *(40)*; volume tables have been published *(9)*.

Rooting Habit—Some confusion exists regarding the rooting habit of saplings and mature cedros. While early workers all reported a very superficial root system, recent literature *(34)* suggests that the species can become deeply rooted if the soil is loose and coarse or fissured. This is compatible with previously reported observations of vigorous cedro growth on old masonry and in light and well-aerated soils. Seedlings, at any rate, are very superficially rooted and may be sensitive to mechanical damage from weeding and other soil preparation activities *(10)*.

Reaction to Competition—Although tolerant of weeds during the seedling stage *(63)*, cedro is classed as intolerant of weeds and shade at the sapling stage and beyond *(34)*. Its thin and spreading crown of light green leaves suggests the habit of a light-demanding species as does its potential for fast growth and its appearance after fire *(34)*, in hedgerows *(40)* and on ruins *(48)*. It is best described as late successional, as it has a moderately long life span. In Trinidad and elsewhere, cedros with more than 100 growth rings are not uncommon *(1,40)*.

Attempts to grow *Cedrela* in plantation systems in Latin America were almost entirely unsuccessful until recently. These early failures *(10, 11,17,23,39,40,51)* have been attributed to poor choice of experimental sites (too wet, wrong soils), increased risk of insect attack in the dense artificial populations *(20)*, and misunderstanding of light requirements *(58)*. However, a few successes may point to fruitful avenues of further experimentation. Under dry conditions, cedar was successfully grown in plantations in Ecuador with no shade and no apparent *Hypsipyla* shootborer problems *(59)*. Successful line plantings have been established in Surinam and the taungya system has been used in Mexico *(42,58)*.

Damaging Agents—Cedro can tolerate some crown damage by hurricanes and will often resprout. Shade-grown seedlings are sensitive to sunscald after which they become more vulnerable to insect attack. Cedro from tropical provenances is not likely to be frost tolerant. Provenances showing frost resistance grow more slowly than tropical provenances *(34,44,57)*.

Plantations of cedro have suffered snail damage in Malaysia and Africa. Slugs killed some nursery stock of an exotic provenance in the Virgin Islands. Beetle damage is a problem in some plantations in Africa, but evidently not in the New World *(34,44,62)*.

The most serious insect pest of cedro is the mahogany shootborer *Hypsipyla grandella (24)*. The larvae of this moth eat the pith just behind the growing tip of fast-growing shoots, causing death of the apical meristem. In turn this slows seedling and sapling growth and may ruin tree form, since multiple leaders or bushiness often result. Shootborer attack may also contribute to seedling mortality, especially in already stressed populations *(3,20)*. Although the borer has been studied extensively *(21,49 63)*, an integrated control system has not yet been developed. It has been observed that pest attacks are least frequent in strongly seasonal climates, where the cycle of insect reproduction is naturally broken at least once a year *(23,63)*. Attack is also less frequent in natural forest where host trees are few and widely scattered, so that large pest populations never build up, under shade as contrasted to full sunlight, and in dormant seedlings *(20,26,62)*. Provenance trials of cedars from a wide geographic range have shown that they may vary in response to attack *(12)* and careful selection may allow future development of tolerant strains. Some progress has been made in chemical and biological control strategies *(2,3, 18,19,22)* but, regardless of the chemicals used, the target insect may eventually develop resistance to them.

Special Uses

Cedro wood is still in considerable demand wherever it is available in the American tropics. An attractive, moderately lightweight wood (specific gravity 0.4), its primary use is in household articles used to store clothing. Cedro heartwood contains an aromatic and insect-repelling resin that is the source of its popular name, Spanish-cedar (it resembles the aroma of true cedars *(Cedrus* spp.). The easily worked wood is both rot-resistant in the ground and highly termite-resistant, making it suitable for exterior construction. Cedro works easily and makes excellent plywood and veneer and would be more widely used if it could be successfully plantation grown *(34,35,48,52)*.

Cedro is an important avenue and shade tree in the West Indies and South America, and where imported, in Africa. It has also been used successfully as cacao and coffee shade in Trinidad.

Genetics

Population Differences

The genus *Cedrela* has undergone two major systematic revisions since 1960. The most recent revision reduced the number of species in the genus to seven *(53)*. The common cedro, *Cedrela odorata* L., embraces 28 other named species, including *C. mexicana* M. J. Roem. The taxon "*C. angustifolia*," a very vigorous type now in demand because of its apparent resistance to the shootborer, was left in an indeterminate status due to insufficient herbarium material. The result is that *C. odorata* as now constituted is a species showing a high degree of population variation. The West Indian material, upon which the original species description was based, is characterized by glabrous foliage with sessile leaflets, whereas the variety (formerly species) "*mexicana*" of Central and South America has varying degrees of pubescence, as well as generally larger leaves with petiolate leaflets, but intermediate varieties exist. Early plantation trials indicated that the variety called "*mexicana*" is faster growing than the West Indian race *(59)*.

Races

Recently completed provenance trials *(7,8,12,13, 14,15,26,32,33,35,44,46,50,62,65)* have suggested that many ecological races of cedro exist. Provenance differences showed up most clearly in African trials, where they were not masked by the adverse effects of the shootborer. Efforts are underway to expand provenance trials to include more seed sources for promising types *(12)*.

Hybrids

Smith *(51)* suggested that the widely distributed species of cedro, *C. odorata* and *C. fissilis*, as well as the doubtful taxon *C. angustifolia* (which he recognized as a separate species), hybridized freely, and that hybrids could explain the great phenotypic variability in these taxa. Unfortunately, there is still no experimental evidence to support or reject the hybridization hypothesis. Recent cytological studies have shown that at least two separate basic diploid chromosome numbers (2n= 50 and 56) occur in *C. odorata*; this occurrence of different intraspecific chromosomal races seems widespread in the Meliaceae and may inhibit free hybridization *(54,56)*.

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Celtis laevigata Willd. Sugarberry

Ulmaceae Elm family

Harvey E. Kennedy, Jr.

Sugarberry (*Celtis laevigata*), a common medium-size tree of moderate to fast growth, is most often found on clay soils of broad flats or shallow sloughs within the flood plains of major southern rivers. It is also called sugar hackberry, hackberry, Texas sugarberry, southern hackberry, and lowland hackberry. Sugarberry is short lived, probably not living more than 150 years. The wood is of medium strength and hardness and much of the light yellow wood is used by furniture manufacturers. The abundant crops of fruits are eaten by wildlife, especially birds. The tree is planted as an ornamental and as a street tree in residential areas in the lower South.

Habitat

Native Range

Sugarberry (figs. 1, 2) ranges south from southeastern Virginia to southern Florida, west to central Texas and northeastern Mexico, and north to western Oklahoma, southern Kansas, Missouri,

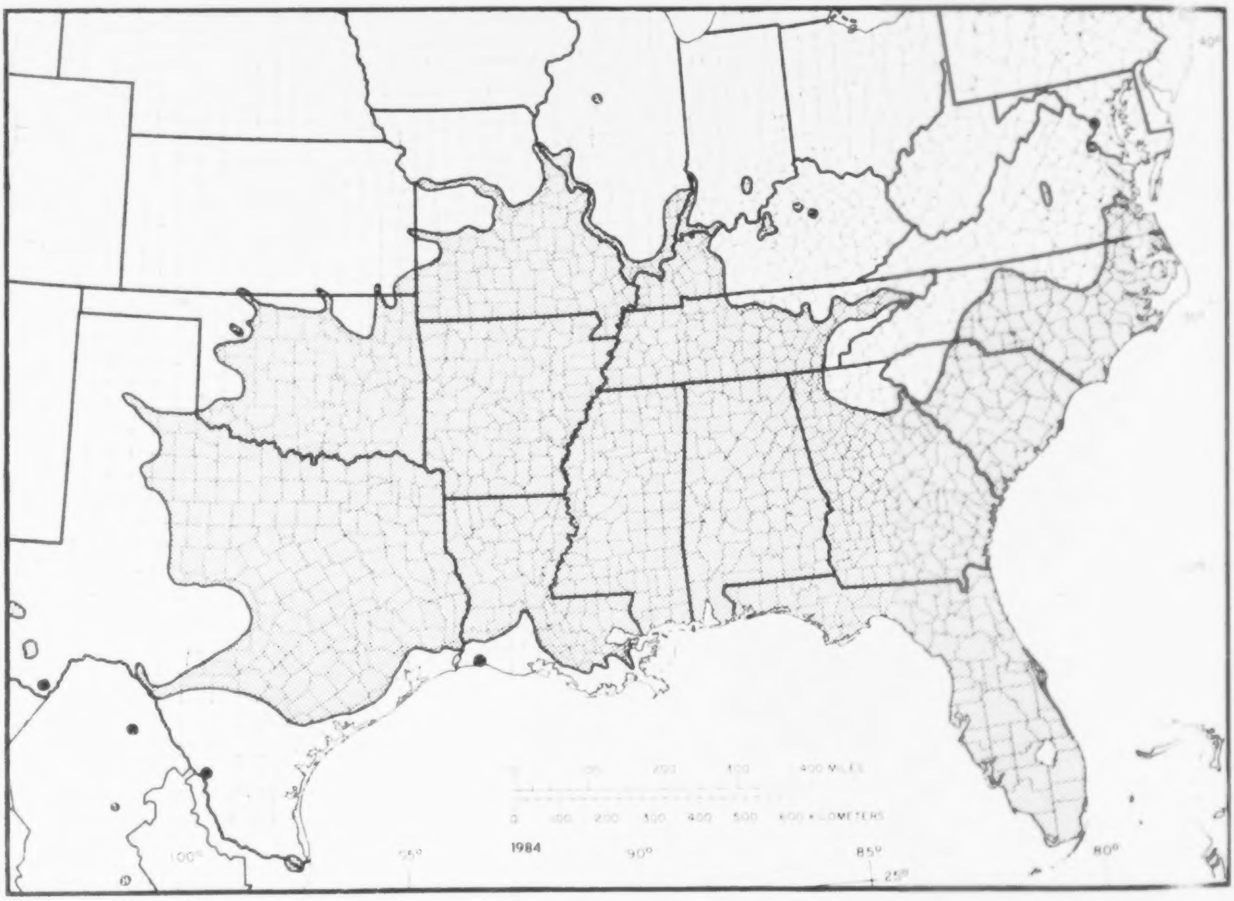

Figure 1—*The native range of sugarberry.*

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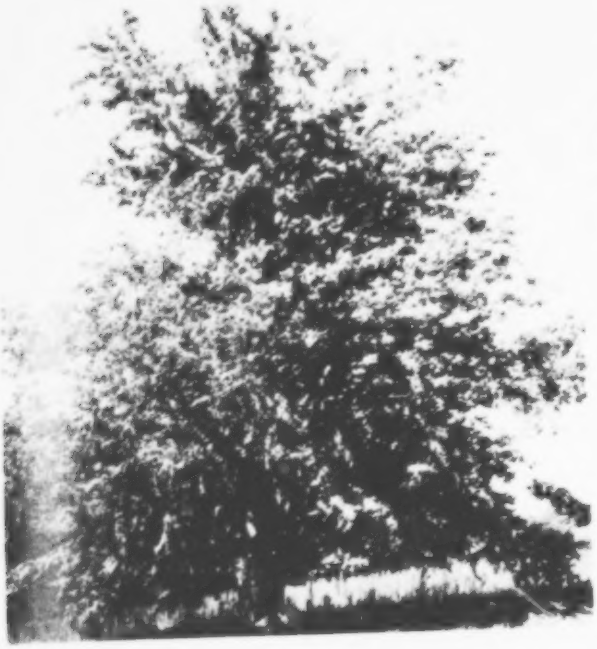

Figure 2—*A medium-sized open-grown sugarberry tree in Louisiana.*

southern Illinois, southern Indiana, and western Kentucky. It is local in Maryland, the Rio Grande Valley, and northeastern Mexico. Its range overlaps the southern part of the range of hackberry (*C. occidentalis*).

Climate

Sugarberry grows in a humid climate except for part of its range in Oklahoma and Texas which lies west of a north-south line through Galveston Bay. There the climate is semihumid to semiarid. The average precipitation varies from 510 to 1520 mm (20 to 60 in) per year, the lightest being in central Texas and Oklahoma. An average of 380 to 760 mm (15 to 30 in) occurs during the frost-free period. Annual snowfall ranges from 0 to 51 cm (0 to 20 in).

Summer temperatures vary from an average of 27° C (80° F) to extremes of 46° C (115° F). Average winter temperatures are from –1° to 10° C (30° to 50° F), with an extreme of –29° C (–20° F).

The average length of the growing season varies from 150 to 270 days.

Soils and Topography

Sugarberry is most common on Inceptisols and Entisols found in broad flats or shallow sloughs within flood plains of major southern rivers (*9*), but will grow under a considerable range of soil and moisture conditions. It is widely distributed on bottom lands except in deep swamps and is found to a minor extent on upland sites. It is also common on deep moist soils derived from limestones, notably in the Black Belt of Alabama (*10*).

Associated Forest Cover

Sugarberry appears with the following forest cover types (*11*): Cottonwood (Society of American Foresters Type 63), Sweetgum-Willow Oak (Type 92), Sugarberry-American Elm-Green Ash (Type 93), Sycamore-Sweetgum-American Elm (Type 94), Black Willow (Type 95), and Overcup Oak-Water Hickory (Type 96).

Other tree associates are cedar elm (*Ulmus crassifolia*), winged elm (*U. alata*), water oak (*Quercus nigra*), blackgum (*Nyssa sylvatica*), persimmon (*Diospyros virginiana*), honeylocust (*Gleditsia triacanthos*), red maple (*Acer rubrum*), and boxelder (*A. negundo*). Some important noncommercial tree and shrub associates are swamp-privet (*Forestiera acuminata*), roughleaf dogwood (*Cornus drummondii*), and hawthorn (*Crataegus* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—The small, greenish flowers appear with the leaves in the early spring—from mid-March to May, depending on latitude (*1*). Sugarberry is polygamo-monoecious. The fruit ripens in September and October, and often remains on the trees until midwinter. Sugarberry fruits are spherical drupes 6 to 13 mm (0.25 to 0.5 in) in diameter with a thin pulp enclosing a single bony nutlet. Late spring frosts sometimes kill the flowers and reduce the seed crop.

Seed Production and Dissemination—Seed production starts when trees are about 15 years old (*7*). Optimum seed-bearing age is from 30 to 70 years old. Sugarberry bears good seed crops in most years and some nearly every year. There are between 4,400 and 5,300 cleaned seeds per kilogram (2,000 to 2,400/lb). The seed is widely dispersed by birds and water.

Mature fruits can be picked by hand from trees as late as midwinter. Collection is easier after trees have completely dropped their leaves. Branches of sugarberry can be flailed to knock the fruits onto sheets of plastic or other suitable material spread under the trees.

If seeds are to be used for seedling production in a nursery, then both fall sowing of untreated seeds and spring sowing of stratified seeds are satisfactory. Seeds may be broadcast or drilled in rows and should be covered with 6 to 13 mm (0.25 to 0.5 in) of firmed soil. Beds should be covered with bird screens until germination starts. Experience at the Southern Hardwoods Laboratory, Stoneville, MS, has shown that if spring sowing is used, the seeds should be depulped before storage, dried to 8 to 10 percent moisture content, and stored in 6-mil-thick plastic bags or equivalent storage containers until stratification. Seeds should be stratified in moist sand or other suitable media for 60 to 90 days before sowing in the nursery. The seeds can be depulped by wet maceration. Depulping is not essential, but it has been reported to aid germination *(1)*. Average germinative capacity is reported to be 55 percent for sugarberry.

Seedling Development—Sugarberry seeds lie dormant over winter and germinate early in the spring. Germination is epigeal *(1)*. The seedlings become established under most stands of southern bottom land hardwoods. Best natural conditions for germination are moist, loamy soil, but the species is found mostly on clay soils. First-year growth usually produces a very slender but tough stem, 20 to 46 cm (8 to 18 in) in height. Under shade, the young seedling develops a crooked, short stem, often forked within a few feet of the ground. In the open, it tends to be very limby and short boled. Sugarberry is considered intolerant of flooding, at least in the seedling stage *(2,3,4)*.

Vegetative Reproduction—Sugarberry can be propagated by cuttings *(7)*. Small stumps sprout readily, and there is some sprouting from root collars of fire-damaged seedlings and saplings.

Sapling and Pole Stages to Maturity

Growth and Yield—Sugarberry is a small- to medium-sized tree. It often attains a height of 24 to 30 m (80 to 100 ft) at maturity. On best sites, 10-year diameter growth can be in excess of 6 cm (2.5 in) for dominant trees *(9)*. The overall average is about 2.5 to 5 cm (1 to 2 in) in 10 years. On average sites, mature forest-grown trees average about 46 cm (18 in) in diameter and 24 m (80 ft) in height, with trunks clear of branches for approximately 9 m (30 ft).

An accurate estimate of the total growing stock is available for only a limited portion of the sugarberry range. Because of its scattered occurrence, forest surveys usually include sugarberry in a group of other species with limited frequencies. The only region containing enough sugarberry of sawtimber size to list separately is the Mississippi Delta *(10)*. The principal States producing commercial quantities of sugarberry are Louisiana, Mississippi, and Arkansas. These States contain about 16 million m^3 (560 million ft^3) and about 9.4 million m^3 (1,650 million fbm) of sugarberry sawtimber. In 1965, a rough estimate of the total sawtimber resource in the United States was in excess of 10.0 million m^3 (2,000 million fbm).

Rooting Habit—Sugarberry is a relatively shallow-rooted tree and does not develop a distinct taproot. The root system is saucer-shaped with good lateral root development. The tree is about average in resistance to windthrow.

Reaction to Competition—Sugarberry is classed as tolerant of shade. It grows fast when released and often outgrows more desirable forest species *(5)*. Sugarberry becomes established in the understory and generally has very poor form in this situation. In dense, even-aged stands, however, it prunes itself well and produces a straight stem.

Damaging Agents—The bark is thin and easily injured by fire. A light burn kills back reproduction. Heavier burns may kill even the largest trees and wound others, making them subject to serious butt rot, which in sugarberry advances rapidly. Butt rot is a common name used to indicate the area of the decay in the butt log which may be caused by any one of 30 or more species of fungi belonging to the genera *Fomes, Polyporus, Hericium,* and *Plyeurotus.*

Ice also causes heavy damage to the crowns, breaking the main stem and branches which reduces growth and creates wounds that allow entrance of rot-causing fungi. There are some other diseases of the twigs and leaves, but none are of major importance.

Eastern mistletoe *(Phoraedendron flavescens)* may cause serious damage in the western part of its range *(7)*. A number of scales attack the twigs, small branches, and sometimes the trunks, but none are considered very damaging. Leaf petiole galls caused by the hackberry petiole gall maker *(Pachypsylla venusta)* are common. In recent years, defoliation of large acreages in several Southern States by larvae of the hackberry butterfly *(Asterocampa celtis)* have been reported *(12)*. No deaths or crown die-back among the trees was observed in the following years. Research has shown that the hackberry butterfly can be controlled by spraying trees with certain registered insecticides *(8)*.

Special Uses

Sugarberry mixed with hackberry supplies the lumber known as hackberry. Small amounts are used for dimension stock, veneer, and containers, but the main use of sugarberry wood is for furniture. The light-colored wood can be given a light- to medium-brown finish that in other woods must be achieved by bleaching.

The dry sweet fruit is eaten by at least 10 species of birds, as well as other game and nongame animals *(13)*.

Sugarberry is often used for street planting in the lower South and is also used as an ornamental in residential areas. A problem in such use is that leachates from the leaves reduce germination and growth of a number of grasses under the trees *(6)*. These leachates have been identified in the soil as ferulic acid, caffeic acid, and p-coumaric acid.

Genetics

Sugarberry seems to present a considerable number of local variations that have prompted some botanists to name a number of varieties, while other botanists feel the distinctions are too slight to warrant such status *(13)*.

Some varieties listed are Texas sugar hackberry, *C. laevigata* var. ***texana***; Uvalde sugar hackberry, *C. laevigata* var. ***brachyphylla***; scrub sugar hackberry, *C. laevigata* var. ***anomala***; small sugar hackberry, *C. laevigata* var. ***smallii***; Arizona sugar hackberry, *C. laevigata* var. ***brevipes***; net-leaf sugar hackberry, *C. laevigata* var. ***reticulata***.

There are no known races or hybrids of sugarberry.

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Celtis occidentalis L. Hackberry

Ulmaceae Elm family

John E. Krajicek and Robert D. Williams

Hackberry (*Celtis occidentalis*), is a widespread small to medium-size tree known also as common hackberry, sugarberry, nettletree, beaverwood, northern hackberry, and American hackberry. On good bottom-land soils it grows fast and may live to 200 years. The wood, heavy but soft, is of limited commercial importance. It is used in inexpensive furniture where a light-colored wood is desired. The cherrylike fruits often hang on the trees throughout the winter providing many birds with food. Hackberry is planted as a street tree in midwest cities because of its tolerance to a wide range of soil and moisture conditions.

Habitat

Native Range

Hackberry (figs. 1, 2) is widely distributed in the eastern United States from the southern New England States through central New York west in southern Ontario to North and South Dakota. Northern outliers are found in southern Quebec, western Ontario, southern Manitoba, and southeastern Wyoming. The range extends south from western Nebraska to northeastern Colorado and northwestern Texas, then east to Arkansas, Tennessee, and North Carolina, with scattered occurrences in Mississippi, Alabama, and Georgia *(7)*.

Because sugarberry (*Celtis laevigata*) and hackberry are so similar, it has been difficult to establish the exact range of either species in the South. Parts of their ranges overlap, with hackberry probably restricted to the upland and sugarberry occupying the bottom land.

Climate

The wide distribution of hackberry is evidence that this species can withstand a variety of climatic conditions *(6)*. Annual precipitation in its growing area ranges from 360 mm (14 in) in the Great Plains to 1520 mm (60 in) in the southeastern United States, and distribution and kind of precipitation differ greatly by seasons.

Hackberry is subjected to great extremes of temperature in the Great Plains where an annual variation of 60° C (140° F) or more is common but variations are more moderate in the Southeast. The length of frost-free season ranges from 120 to 250 days within its growing area.

Hackberry is drought resistant and has survived extremely dry periods in the Great Plains. During the severe drought of 1934 in western Kansas, hackberry survived better than American elm (*Ulmus americana*) and honeylocust (*Gleditsia triacanthos*), to the same degree as boxelder (*Acer negundo*) and black locust (*Robinia pseudoacacia*), but not as well as bur oak (*Quercus macrocarpa*) and eastern redcedar (*Juniperus virginiana*).

Soils and Topography

Hackberry grows in many soils, and although principally a bottom-land tree, it is frequently found on limestone outcrops or limestone soils. In western Nebraska, hackberry grows on the north side of sand dunes and in river valleys.

Sites with a permanently high water table are unfavorable for hackberry, although periodic flooding apparently is not detrimental. In Kentucky, 46 days of flooding during one growing season caused no apparent damage to this tree. Hackberry begins to show ill effects from inundation after 110 days. If the duration of flooding is less than 25 percent of the growing season, *Celtis* spp. can maintain good health indefinitely. Hackberry trees often survive the first season of permanent flooding but usually die during or after the second season *(8)*. Occasional trees have lived 3 years under flooded conditions. In Illinois, continuous flooding to a depth of 91 cm (3 ft) killed hackberry in less than 4 years. Where only mud was present, 70 percent of the trees were dead at the end of 6 years. Submergence for short periods kills many seedlings. In Pennsylvania, the presence of hackberry has been regarded as an indicator of high (7.2) pH.

Hackberry grows best on valley soils, but throughout much of its range it is also commonly found on slopes and bluffs. In the western part of its range, however, it is restricted to well-developed river valleys, north slopes, and protected ravines, and it is largely absent from windswept parts of the western river valleys. It is common in eastern Iowa on all but the wettest bottom-land sites, and seedling and sapling hackberry occur on upland sites under existing oak stands on all aspects, slopes, and ridges

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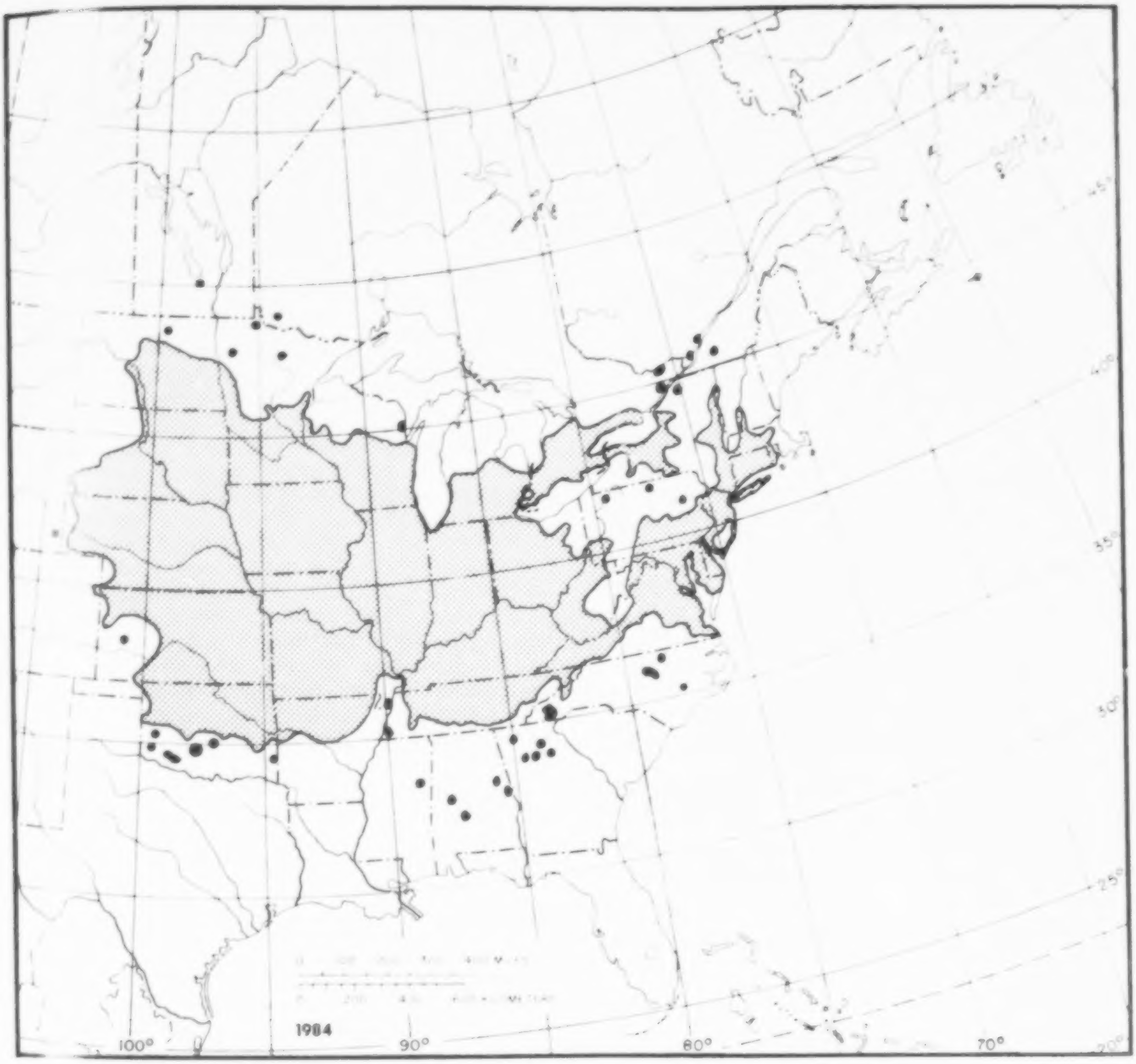

Fig[illegible]1—*The native range of hackberry.*

*(6[illegible]*he soils upon which hackberry grows fall pr[illegible]ily within the soil orders Mollisols, Entisols, an[illegible] a lesser extent, Inceptisols.

As[illegible]iated Forest Cover

[illegible]kberry is seldom found in pure stands in the fo[illegible] It is prominent, however, in the northern ph[illegible] of the forest cover type Sugarberry–American Elm–Green Ash (Society of American Foresters Type 93) where it replaces sugarberry *(4)*.

Hackberry is a common associate in limited portions of three other forest cover types: Sugar Maple–Basswood (Type 26) in the Central Hardwood Region, Beech–Sugar Maple (Type 60) throughout the Midwest, and Sycamore–Sweetgum–American Elm (Type 94) in the Northern Mississippi Valley.

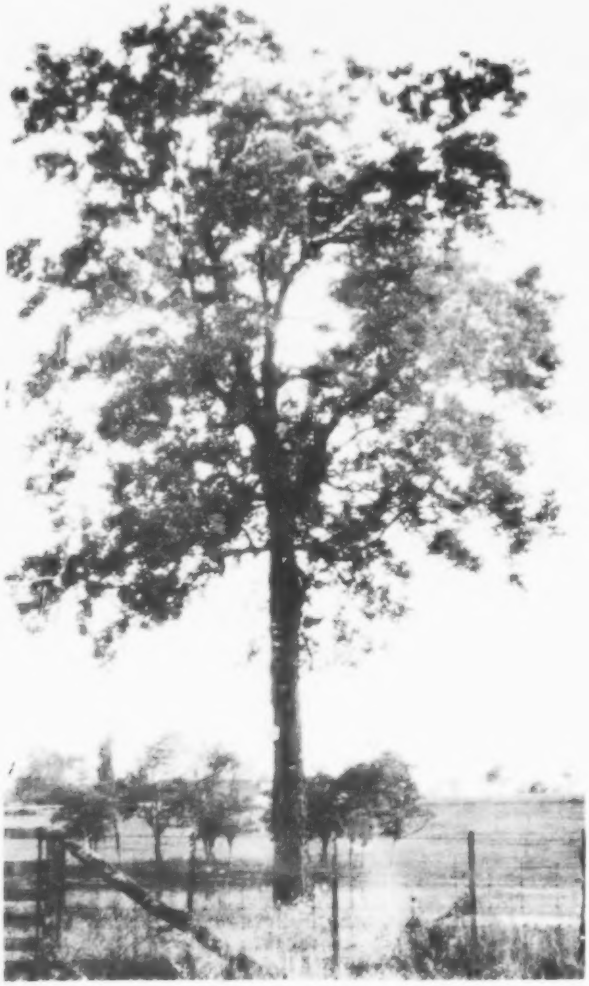

Figure 2—*Open grown hackberry develop ragged, irregular oval crowns.*

Life History

Reproduction and Early Growth

Flowering and Seed Production—Hackberry is polygamo-monoecious. The small greenish flowers *(1)* appear with or shortly after the leaves in early April in the southern part of the range and in late May in the northern part. The seed ripens in September and October, sometimes remaining on the tree until the following spring. The fruit (a spherical drupe) is usually from 6 to 8 mm (0.25 to 0.33 in) in diameter and dark red to purple when ripe. A thin pulp encloses a single bony nutlet.

Hackberry bears good seed crops in most years and light seed crops on intervening years. The seed is disseminated principally by birds and small mammals, but some may be dispersed by water. In an Indiana study, 34 percent of the hackberry seed stored 1 year in the leaf litter germinated and 20 percent of the seed germinated after being stored 2 winters *(3)*.

Seed Production and Dissemination—No information available.

Seedling Development—Germination of hackberry is epigeal *(1)*. In eastern Iowa, hackberry seedlings become established in existing hardwood stands but rarely in old fields. In Illinois, however, the tree has become established in prairie conditions. In Pennsylvania, hackberry seedlings were found in dense shade where seedlings of the other overstory trees did not persist. On an Indiana floodplain, however, hackberry was the only tree of the principal crown cover that had a high rate of mortality among its seedlings.

Early growth of hackberry varies greatly within its range and even on different sites in a single locality. Although height growth may not exceed 2.5 cm (1 in) per year under a dense overstory, cultivated hackberry planted in the Great Plains shelterbelts averaged 0.4 m (1.3 ft) per year during the first 6 years *(6)*.

Vegetative Reproduction—Hackberry can be propagated by stem cuttings, grafting, budding, and by layering. Sprouts develop from stumps of small trees but rarely from those of large ones.

Sapling and Pole Stages to Maturity

Growth and Yield—On the better alluvial soils, diameter growth of hackberry may be as much as 8 mm (0.3 in) annually, although usually it is much less. In the western part of its range, an annual diameter growth of 5 mm (0.2 in) has been observed. Usually growth is most rapid between the 20th and 40th years. On poor sites, growth is very slow and the trees are often dwarfed.

Mature hackberry is usually a small- to medium-sized tree from 9 to 15 m (30 to 50 ft) tall and from 46 to 61 cm (18 to 24 in) in d.b.h. *(6)*. On the best sites, however, it may reach a height of 40 m (130 ft) and a d.b.h. of 122 cm (48 in). Trees up to 29 m (95 ft) tall and 122 cm (48 in) in d.b.h. have been found in the western part of the range. Maximum age attained by hackberry is probably between 150 and 200 years.

Rooting Habit—Hackberry is a deep rooting species, ultimately reaching depths between 3 and 6 m (10 and 20 ft) on most sites *(8)*. On clay prairie soil in North Dakota, however, the roots reached only to a depth of 1.4 m (4.5 ft); lateral extension was 12.6 m (41 ft). Strong taproots develop only occasionally.

The root anatomy of the genus *Celtis* is unique, along with a few other genera, in that a primary structure of the root phloem is stereome (sclerenchyma and collenchyma collectively). Stereome seldom develops in roots and when present is usually a secondary structure. The mycorrhizal associates of hackberry are the ectomycorrhizae *(8)*.

Mature hackberry is classified as moderately tolerant of flooding. New seedlings are much more sensitive to saturated soil conditions than older trees. The root systems of hackberry seedlings in saturated soil are severely injured within 60 days and are often unable to recover. Intolerance of flooding is attributed to injury to the root system, lack of strong adventitious roots, and the inability of the stems and leaves to resist desiccation due to a poorly or nonfunctioning root system.

Reaction to Competition—Hackberry is intermediate to tolerant in its ability to withstand shade *(6)*. Trees suppressed for an extended period are often poorly formed.

Because hackberry is found in many forest types ranging from temporary to subclimax, its successional position is difficult to determine. Where it occasionally grows in small, nearly pure stands, it is probably only a temporary type.

Damaging Agents—Hackberry is the host of four gall-producing insects—*Pachypsylla celtidisgemma*, *P. celtidismamma*, *P. celtidisvesicula*, and *P. venusta*. The adults pass the winter in cracks of the bark or among the debris on the ground and in spring lay eggs on the leaves. The damage is not serious.

The hackberry engraver *(Scolytus muticus)* normally attacks only dead or dying branches but has been reported to attack the living sapwood thus killing the tree.

Several leaf-spot fungi are common on hackberry trees: *Cercospora spegazzinii*, *Cylindrosporium defoliatum*, *Cerosporella celtidis*, *Mycosphaerella maculiformis*, *Phleospora celtidis*, *Phyllosticta celtidis*, and *Septogloeum celtidis*. The most important disease is "witches-broom," which causes a rosette-like proliferation of the branch tips and is caused by two agents, one the gall mite *Eriophyes* spp. and the other a powdery mildew *(Sphaerotheca phytophila)* *(5)*. Hackberry is highly susceptible to fire damage, which opens the way for wood decay organisms.

Armillaria mellea grows unaggressively on hackberry roots until they die or are injured, whereupon the fungus enters and causes extensive root rot.

Special Uses

Hackberry seed is eaten by animals, and in Kansas the fox squirrel feeds on both the nipple galls and the fruit. The fruit is eaten also by quail, ring-necked pheasant, wild turkey, cedar waxwings, sharp-tailed grouse, yellow-bellied sapsuckers, mockingbirds, robins, and other birds.

Good grades of hackberry wood are used for furniture, millwork, and some athletic equipment. Poor grades are used for crates and boxes.

Genetics

Because hackberry grows in a region with great climatic differences, genetic variation probably exists; however, provenance tests have just begun in the Great Plains area.

Although no hybrids have been reported, it has been noted that *Celtis occidentalis* and *C. laevigata* are self-compatible and therefore capable of hybridizing *(2)*.

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Cercis canadensis L. Eastern Redbud

Leguminosae Legume family

James G. Dickson

Eastern redbud (*Cercis canadensis*) is a small, short-lived deciduous tree found throughout the eastern United States. Redbud is also known as Judas-tree. According to legend, Judas Iscariot hanged himself from a branch of the European species *Cercis siliquastrum* (*13*). Eastern redbud is a strikingly conspicuous tree in the spring because it flowers before other tree leaves form. The wood is heavy, hard, and close-grained, but because of the small size and irregular shape of the tree it is of no commercial value as a source of lumber. This tree is most valued as an ornamental and is extensively planted.

Habitat

Native Range

The range of eastern redbud (figs. 1, 2) is from New Jersey and southern Pennsylvania northwest to southern Michigan, southwest into southeastern Nebraska, south to central Texas, and east to central Florida (*8*). A disjunct population of redbud extends from the Trans-Pecos and south Texas into Mexico.

Climate

A wide range of climatic conditions are present in the large geographical range of redbud. Mean annual precipitation is less than 510 mm (20 in) in dry south Texas and approximately 1270 mm (50 in) in moist central Florida. Mean annual snowfall in the northern perimeter of redbud is about 90 cm (35 in). Mean January temperatures vary from -8° C (18° F) to 16° C (61° F) within the native range of redbud. Mean July temperatures vary from about 21° C (70° F) in southern Pennsylvania to 26° C (79° F) in central Florida. Frost-free days can vary from 160 to 300 days.

Soils and Topography

Redbud is found on a variety of sites ranging from xeric to mesic but grows better on moist, well-drained sites. It is normally more abundant on south-facing slopes where sunlight is more intense and there is less plant competition (*11*). This species does not usually grow on flooded sites because it cannot endure inundation or survive in poorly aerated soils.

The tree grows well in a variety of soil textures but is not found in coarse sands (*11*). It requires some fine or colloidal material. Redbud is tolerant of a wide pH range but grows best where the pH is above 7.5. It is prevalent on limestone outcrops and on alkaline soils derived from them (*11,12*). Redbud is tolerant of nutrient deficiencies. Therefore, less competition can occur from associated trees that are less vigorous on the nutrient deficient sites. In Indiana no relationship was noted between distribution of redbud and soil calcium or magnesium. Redbud is found on soils of most soil orders, but most commonly on those of the orders Alfisols and Mollisols.

Associated Forest Cover

Redbud is a regular but usually not a common understory component of many forest types throughout the Eastern United States. It is not a commercial timber species, and although it grows in many forest cover types, it is not listed in all of them by the Society of American Foresters (*4*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Redbud flowers are pink to reddish purple, and rarely white. They are borne on pedicels in clusters of two to eight. Flowers are produced from small buds on old twigs, branches, and trunks. Flowers are bisexual and the tree is self-pollinating. Flowering usually occurs sometime from March to May and precedes leafing. In Indiana, the tree requires 30 days of temperatures averaging more than 10° C (50° F) . Previous winter chilling also enhances flowering (*11*). Pollination is usually accomplished by bees. After 2 or 3 weeks leaves appear and the flowers drop. The ovaries of one to several flowers in most flower clusters enlarge and develop into fruits that reach their full size by midsummer (*13*). Fruits are flat reddish-brown pods about 1.3 cm (0.5 in) wide and 5 to 10 cm (2 to 4 in) long (*16*). Each fruit contains 4 to 10 brown, hard, compressed beanlike seeds, each about 6mm (0.25 in) long. The fruits remain on the tree until after leaf fall; some persist throughout winter (*15*).

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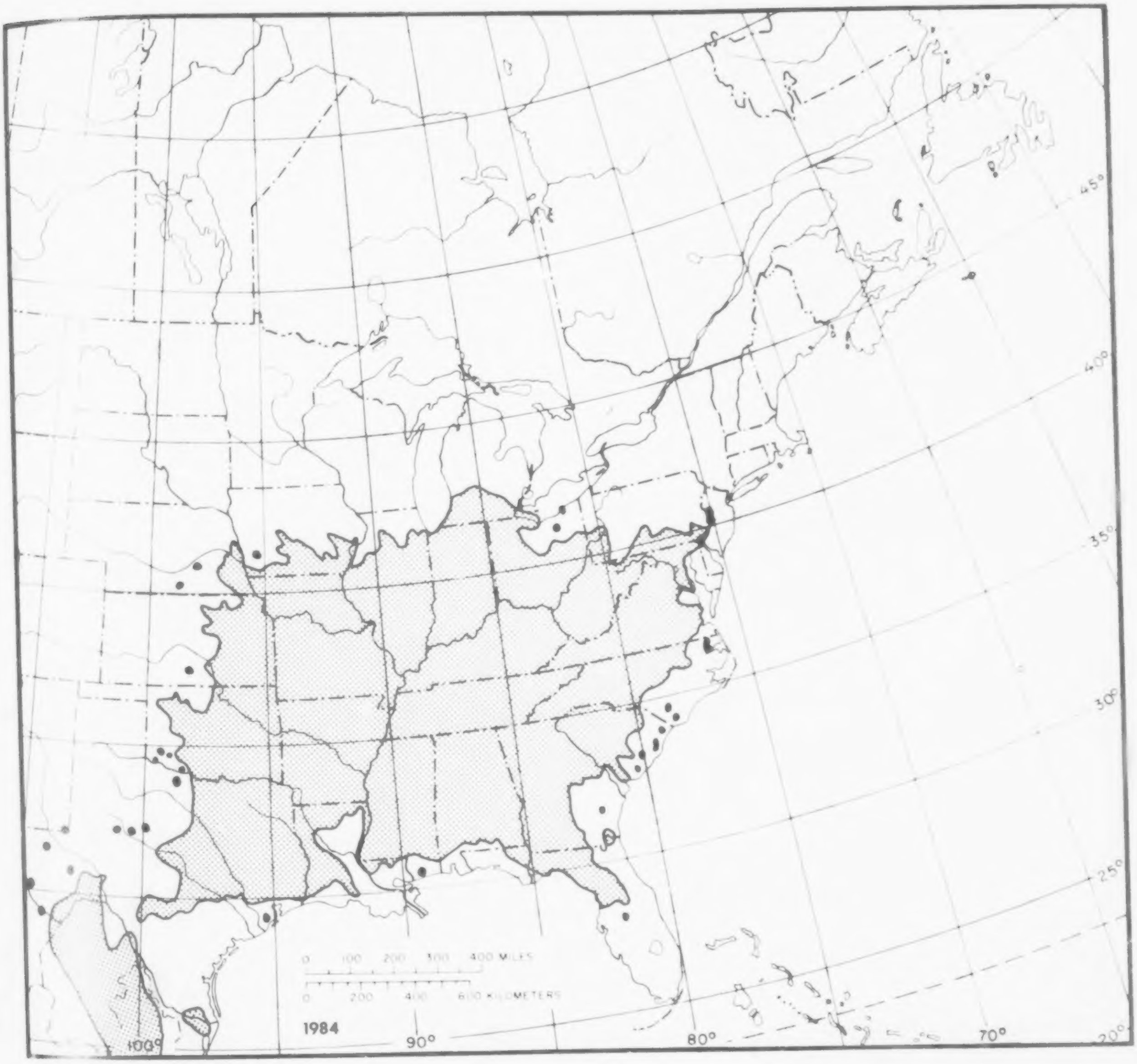

Figure 1—*The native range of eastern redbud.*

Seed Production and Dissemination—Seeds are released by the opening of fruit sutures or decay of the fruit wall. Most seeds are dispersed during fall and winter by wind and animals. Many seeds are injured by insects. Those that fall to the ground usually remain dormant for several years *(1)*.

For artificial propagation, seeds should be collected, cleaned, and dried when ripe to avoid insect damage. Dried seeds can be stored in sealed glass or metal containers at 2° to 5° C (35° to 41° F). Seed treatment is necessary for propagation because redbud shows delayed germination due to impermeability of the seed coat to water and dormancy of the embryo *(1)*. The seed coat can be made permeable to water by mechanical scarification or by immersion in boiling water or in concentrated sulfuric acid for

Figure 2—*Eastern redbud makes a handsome ornamental year-round.*

about 30 minutes. After scarifying, seeds should be stratified in moist sand at about 5° C (41° F) for 5 to 8 weeks *(14)*.

Prepared seeds should be sown in well-prepared seedbeds in late April or early May *(14)*. Moist soil should cover seeds at a maximum depth of 0.5 cm (0.2 in). Propagation can also be accomplished by layering or cuttings.

Seedling Development—Approximate site characteristics and seedling vigor determine seedling establishment. Germination is epigeal *(14)*. Under optimum conditions seedlings can grow 0.3 m (1 ft) in height the first growing season. Continuous terminal growth is related to light intensity, photoperiod, and temperature *(11)*. Once established, seedlings can endure much shading.

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—Development of young redbud to the flowering stage is rapid. Young redbuds have been observed first flowering when less than 7 years old but do not fruit the first year of blossoming. Annual cambial growth begins just before flowering and shoot growth usually begins during flowering *(11)*. In Indiana terminal growth of saplings started when the weekly mean of the daily mean temperature reached 13° C (55° F). Maximum growth was reached the fourth week and growth ceased after 6 to 10 weeks under low soil moisture conditions. With adequate soil moisture, terminal growth continued until frost. More than 1076 lux (100 lumens/ft^2) of light and more than 13 hours of daylight daily are needed to maintain terminal growth of saplings.

Rooting Habit—Redbud develops a deep taproot that descends rapidly the first few years if the soil permits. Initial growth depends on soil moisture and the absence of a tight clay subsoil. If impenetrable subsoils are present the taproot grows horizontally. Secondary roots appear when the taproot is 5 to 8 cm (2 to 3 in) long and grow rapidly.

Reaction to Competition—As redbuds grow and mature they become less shade tolerant. Old trees usually suffer from heart rot and cannot normally tolerate severe competition and shade. Redbud is most accurately classed as tolerant of shade.

Damaging Agents—Redbud is a host to a variety of insects, but damage is not normally severe. Bark and phloem borers include three species of *Hypothenemus*, and *Pityophthorus lautus (2)*. A seed beetle, *Gibbobruchus mimus*, breeds in the seed of redbud.

Numerous wood borers have been found in redbud. *Agrilus otiosus*, three species of *Hypothenemus*, three species of *Micracis*, two species of *Microcisella*, *Pityophthorus lautus*, *Ptosima gibbicollis*, and *Thysanoes fimbricornis* all inhabit portions of the wood of redbud.

Other insects feed on the leaves of redbud. The redbud leaffolder, *Fascista cercerisella*, feeds on leaves which the larvae web together. The grape leaffolder, *Desmia funeralis*, an important pest of grape, also feeds on redbud. The Japanese weevil, *Callirhopalus bifasciatus*, and *Norape ovina* both consume redbud leaves.

Other insects feed on redbud by extracting juices from the plant. The twolined spittlebug, *Prosapia bicincta*, has been recorded feeding on redbud. The terrapin scale, *Mesolecanium nigrofasciatum*, and San Jose scale, *Quadraspidiotus perniciosus*, like most of the other redbud parasites, inhabit a variety of hosts including redbud. The periodical cicada, *Magicicada septendecim*, lays its eggs in more than 70 species of trees and other plants, including redbud.

There are three main diseases of redbud: leaf anthracnose, ***Mycosphaerella cercidicola***, Botryosphaeria canker, and Verticillium wilt *(6)*. The most serious is the canker *Botryosphaeria ribis* or its variety *chromogena*. The species is mainly a saprobe; the variety is a parasite. This variety produces stem and twig lesions and entire groves of redbuds have been killed by this disease. Verticillium wilt *(Verticillium albo-atrum)* sometimes kills redbuds, especially in the Midwestern United States. Redbud is vulnerable to Texas root rot *(Phymatotrichum omnivorum)*, but redbud is not commonly grown in its range. A variety of sap and heart rots also infect eastern redbud.

Special Uses

The eastern redbud is extensively planted as an ornamental throughout the Eastern United States. It is tolerant of a wide range of site conditions, is not especially vulnerable to insects or diseases, is relatively easy to maintain, and makes a beautiful shrub or small tree, especially when flowering.

Bark of redbud has been used as an astringent in the treatment of dysentery. Flowers of the tree can be put into salads or fried and eaten *(16)*. There is some documented wildlife use of redbud fruit. Cardinals have been observed feeding on the seeds, and seeds have been consumed by ring-necked pheasants, rose-breasted grosbeaks *(5)*, and bobwhites *(7)*. White-tailed deer and gray squirrels have also been observed feeding on the seeds *(5)*. Flowers of the tree are regarded as important in the production of honey by bees *(10)*.

Genetics

Donselman *(3)* investigated morphological variation in trees grown from seed collected from 13 diverse locations in the range of redbud. He concluded that trees from more xeric locations in the southwestern and western portions of the range exhibited adaptations to high solar radiation, drying winds, low humidity, low soil moisture, and other environmental factors associated with high evapotranspiration. Leaves from those plants were thicker and smaller, had increased pubescence, and showed more efficient stomatal geometry than trees from mesic locations.

Two subspecies of redbud have been identified: Texas redbud *(Cercis canadensis* var. *texensis)* found in southern Oklahoma, Trans-Pecos Texas, and southeastern New Mexico; and eastern redbud *(C. canadensis* var. *canadensis)* found in the remainder of the range of redbud *(9)*. Another native *Cercis* species, California redbud *(C. occidentalis)*, is found in Utah, Nevada, California and Arizona.

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Cordia alliodora (Ruiz & Pav.) Oken   Laurel, Capá Prieto

Boraginaceae   Borage family

L. H. Liegel and J. W. Stead

Laurel *(Cordia alliodora)* is a tropical hardwood that grows from Mexico to Argentina. It is also known as capá prieto. The species frequently serves as shade for coffee trees and farm animals. The wood is easy to work and the dark colored heartwood is a favorite of woodworkers for fine carpentry.

Habitat

Native Range

Laurel is the most widely distributed species of *Cordia*, a genus including some 200 species ranging from shrubs to large trees. The geographic range is quite extensive, from latitude 25° N. to 25° S., or roughly from the State of Sinaloa in Mexico to Misiones in Argentina *(30)*. The range also includes most of the West Indies *(16)*. Laurel is thought to have been introduced to Jamaica *(13)* and was first planted in Surinam as an exotic plantation species in 1967 *(36)*. It has also been planted as an ornamental in Florida *(16)*. Local distribution maps are not generally available, except for Mexico *(7)*, Colombia *(37)*, and Puerto Rico *(16)* where ranges are given for both geographical and political regions. In Puerto Rico laurel grows in more than half of the municipalities, in 8 of 13 State Forests, and in the Luquillo Experimental Forest Biosphere Reserve.

Climate

Laurel reportedly grows best in Tropical Moist to Tropical Wet Forest life zones *(11,12)* where mean annual rainfall ranges from 2000 to 5000 mm (80 to 200 in) and mean annual temperature is 24° C (75° F). But in Trinidad *(21)* best growth of laurel was observed outside rain forests where annual rainfall was between 1270 and 1900 mm (50 to 75 in). The natural distribution of laurel in Puerto Rico seemed to follow this trend *(19)*. In Central America and the West Indies, laurel grows in Tropical or Subtropical Dry Forest life zones; mean annual rainfall is about 750 to 2000 mm (about 30 to 80 in) and mean annual temperature is from 25° to 27° C (77° to 81° F). Growth is much slower and form is less impressive in the drier areas. In Puerto Rico laurel grows mainly in coastal Subtropical Moist Forest or in the Subtropical Wet Forest uplands *(17)* where mean annual rainfall ranges from about 1000 mm (40 in) to 3500 mm (138 in) or more. Less frequently in Puerto Rico it occurs in Subtropical Dry Forest where mean annual precipitation is between 600 and 1000 mm (24 and 40 in).

Soils and Topography

The altitudinal range of laurel is broad, from almost sea level in several countries, including Puerto Rico, up to 2000 m (6,560 ft) in the Colombian highlands. More commonly, it grows below 500 m (1,640 ft). Laurel grows best on well-drained, medium-textured soils and does not tolerate either poor internal drainage or water-logging. But it is not exacting in nutrient requirements, adapting well to degraded and abandoned areas once used for row crops, pasture, or shifting cultivation. Topography suited to laurel ranges from flat coastal lowlands, having deep infertile sands and little organic matter (Entisols or Oxisols), as in Surinam *(36)*, to very dissected mountainous uplands, with deep, fertile volcanic soils high in organic matter (Andepts–Inceptisols), as in Colombia and Costa Rica *(29)*. In Puerto Rico, laurel grows on shallow soils of the moist volcanic uplands (Inceptisols), on deep-red clay soils of the moist to wet volcanic uplands (Ultisols), and on shallow soils over limestone (Alfisols).

Associated Forest Cover

Laurel is associated with other pioneer species common to roadsides or gaps in mature forests, gallery forests, or savannas that are subject to natural or human disturbances. Some of these, yagrumo hembra or trumpet-tree *(Cecropia peltata)* and yagrumo macho or matchwood *(Didymopanax morototoni)*, have extensive ranges that overlap that of laurel throughout the West Indies and the tropical Americas. In the Subtropical Dry Forest of Puerto Rico, laurel grows with almacigo or turpentine tree *(Bursera simaruba)*, guayacan or common lignumvitae *(Guaiacum officinale)*, and the common naturalized exotics, bayahonda or mesquite *(Prosopis pallida)* and tamarindo *(Tamarindus indica)*. In Subtropical Moist Forest it is associated with roble blanco or white-cedar *(Tabebuia heterophylla)*, cedro hembra or Spanish-cedar *(Cedrela odorata)*, algar-

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robo or West-Indian-locust *(Hymenaea courbaril)*, jaguey blanco or shortleaf fig *(Ficus laevigata)*, and the common naturalized exotics, flamboyan or flamboyant tree *(Delonix regia)* and caoba dominicana or small-leaf mahogany *(Swietenia mahagoni)*. It also grows on disturbed tabonuco forest type *(Dacryodes excelsa)* along with yagrumo macho and guano or balsa *(Ochroma pyramidale)*. Tabonuco is the mature natural forest remnant of Subtropical Wet Forest *(17)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—In Costa Rica, laurel reaches sexual maturity within 5 to 10 years *(12)*. Some Costa Rican provenances have flowered at 4 years and produced viable seed at 5 years when planted in Surinam *(36)*.

Flowers are perfect and crowded on a widely branched terminal panicle 10 to 30 cm (3.9 to 11.8 in) across. The calyx is cylindrical with 11 prominent ribs. The corolla is white with persistent oblong lobes 5 to 7 mm (0.2 to 0.3 in) long and 1.5 to 3.5 mm (0.06 to 0.14 in) wide. There are five white stamens that are erect and protrude well beyond the exserted style, which is two-forked, each fork having two broad stigmas *(16,30)*.

Overall phenology is quite variable across the range, a common phenomenon for tree species having such extended ranges. Major flowering in Central America occurs from February through March *(30)* and extends through May at least in Costa Rica *(24)*. In the southern part of the range, as in Surinam, flowering occurs earlier, from December through January *(36)*. In Puerto Rico there are no marked wet or dry seasons, and flowering takes place in almost any season *(16)*. Laurel flowers throughout the year in Colombia and Ecuador too, but there is altitudinal variation; the high wet areas flower early in the year, and low dry areas flower later on, into July and August *(23)*. Pollination is by wind or Lepidoptera, and perhaps by bees *(12)*. Trees bear masses of flowers that are quite conspicuous from great distances. If surveys are synchronized with anticipated flowering times, regional or local distributions can be determined easily and with reasonable accuracy *(30)*.

Fruits are cylindrical and ripen within 1 to 2 months after flowering commences. Nutlets are oblong, one-seeded, about 6 mm (0.25 in) long. Seeds are wind dispersed, yet they can persist on the trees a few weeks after ripening. Seedfall is usually quite variable since laurel flowers throughout the year. In Central America maximum seedfall is usually in April and May *(33)*.

Seed Production and Dissemination—A persistent corolla acts as a parachute for seed. Individual trees produce 2 to 8 kg (4.4 to 17.6 lb) of seeds at 42,000 to 100,000 seeds per kg (19,100 to 45,400 seeds/lb) *(30,33,36)*. Based on provenance collection work by the Oxford Forestry Institute (OFI) at Oxford University in the United Kingdom *(30)*, the optimum procedure is threefold:

1. Collect fruits when they change color from green to brown by shaking the entire tree or individual branches so that seeds or fruits fall onto netting or sheets. Under normal conditions the shaking and collection process should precede natural seedfall by 2 to 3 weeks. Only ripe seeds should be collected; fruits should not be pulled off branches.
2. Reduce seed moisture content to 10 percent or less by drying in forced-draft ovens at about 70° C (158° F). In OFI experience, seeds collected by shaking before natural seedfall usually have a moisture content of 10 percent or less. Evidence from Costa Rica suggests that sun drying may be harmful to seeds.
3. Store seeds at low humidity and temperature near 5° C (41° F) in screwtop containers. Unrefrigerated seeds can lose all viability within 5 or 6 months *(33)*. Seeds collected and processed according to OFI recommendations have maintained good viability and shown 50 to 70 percent germination after 3 years in storage. When withdrawn from refrigeration, seeds should be germinated soon afterwards *(30)*.

Seedling Development—Germination is epigeous. Seeds of laurel (fig. 1) germinate within 5 to 20 days after seedfall if there is sufficient soil moisture and a good mineral seedbed. Germination and nursery practices vary among countries currently planting laurel for research or commercial purposes. Wildling stock was successful in Puerto Rico in the late 1940's *(20)*. Planting on mounds and plowing or burning with subsequent protection of sown seeds has been successful in Costa Rica *(31)*. In Surinam, seeds are sown directly into plastic bags or young seedlings are dug up from specially prepared seedbeds located directly beneath designated seed trees *(36)*. In Colombia, seeds are directly seeded onto nursery beds. The yield is about 20,000 seedlings per kilogram (9,100/lb) of seed, but only the most vigorous seedlings are transplanted into plastic bags from germination trays *(29)*.

Several kinds of soil mixtures have been used for nursery beds or bagged seedlings. These include clay

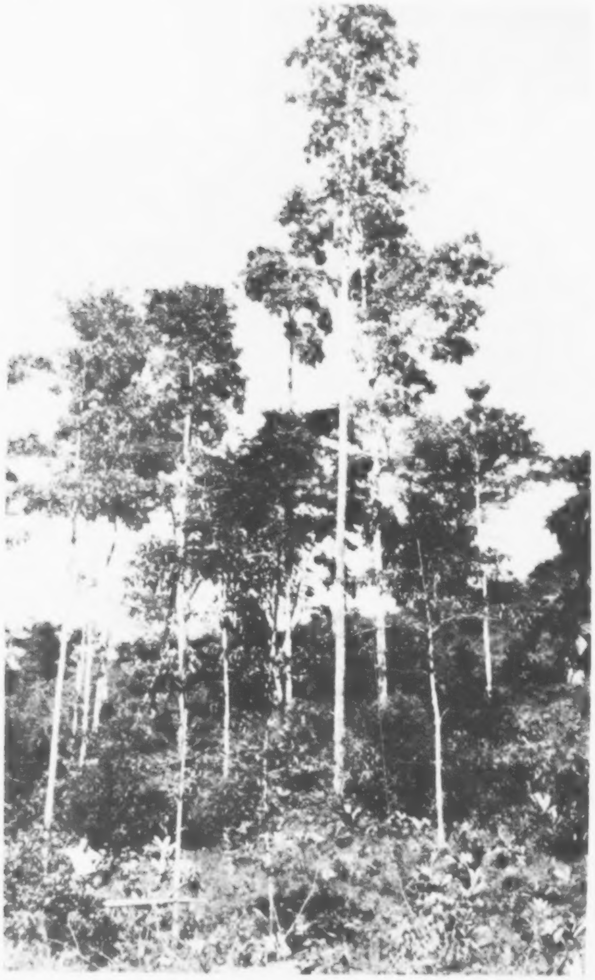

Figure 1—*Natural regeneration of laurel in Limon Province, Costa Rica.*

in Belize; sterilized, washed riversand in Nepal; well-tilled, fertile subsoil in Colombia; and a mixture of equal parts of clay, sand, and black earth in Brazil *(30)*. In Colombia, germination has been poor using sand/soil mixtures *(2)*. Small-grained vermiculite has been more successful in Costa Rica than conventional sand or loam soils *(12)*. There seem to be no particular requirements for sterilization of soils.

Little consistency appears yet in determining optimum seedling size for transplanting or outplanting *(30)*. Reported transplanting criteria for seedlings are 3 cm (1.2 in) tall in Brazil, 14 days old in Nigeria, 2 months old in Belize, the four-leaf stage in Ecuador, and the two-full-leaf stage in Fiji. Outplanting has been done after seedlings spent 10 months in the nursery in Belize, 5 months in Liberia, 5 to 8 months in Surinam, and 2 to 6 months in Costa Rica *(30)*. Outplanted seedlings in Colombia are at least 15 cm (5.9 in) tall, and the recommended minimum lower stem diameter is 20 mm (0.8 in) *(30)*. Stump planting, using a lifted seedling trimmed to 10 to 15 cm (4 to 6 in) of roots and 5 to 15 cm (2 to 6 in) of stem, is now probably the most preferred outplanting technique.

Initial seedling growth after outplanting is usually rapid. Plants have grown about 2 to 3 m (7 to 10 ft) per year after 3 years in Surinam *(36)*. Single individuals from Trinidad and Costa Rica were 7 m (23 ft) and 11 and 17 cm (4 and 7 in) in d.b.h. after 3 years *(12)*. A 2-year-old planting in Colombia averaged 1.9 m (6.2 ft) in height and had 86 percent survival *(3)*. After 7 years mean annual height growth was 2.6 to 2.9 m (8.5 to 9.5 ft) on sands and 2.0 to 2.2 m (6.6 to 7.2 ft) on heavier textured soils in Surinam *(36)*.

Fertilizers have been unsuccessful in improving juvenile height or diameter growth *(12)*. In one trial, several combinations of nitrogen, phosphorus, and potassium did not affect either height or diameter growth of laurel in Costa Rica. In another trial, growth of laurel seedlings 1 year after outplanting was not significantly different between unfertilized and fertilized plots of laurel alone or between fertilized and unfertilized plots with laurel planted with maize *(5)*.

At least two laboratory observations have shown that light and temperature affect seedling growth *(12)*, the best regime being a long (14.5 hr) day and high constant temperature, 30° C (86° F). Height growth occurs in periodic flushes during the growing season; when branches are elongating, terminal growth is slow. Cambial activity begins as the terminal initiates flushing. In Costa Rica, growth rings are almost always annual *(32)*. However, boundaries between summer and early wood are not always distinct or abrupt so that several disks from different bole levels are usually needed to detect all growth rings.

Vegetative Reproduction—Coppicing and epicormic branching on injured young trees have been reported in Costa Rica *(12)*. Sprouting was seen from lateral roots in Trinidad *(21)*. But research in this particular area seems nonexistent except for use of stem and branch sets in laurel tree improvement work in Colombia *(14,35)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature laurel is a medium to large tree. Under optimum growing conditions it may reach 30.5 m (100 ft) and about 100 cm (36 in) in d.b.h. *(12)*. More commonly, it is 20 m (66 ft) high and 46 cm (18 in) in d.b.h. The bole is cylindrical and erect, with whorled branches appearing in horizontal layers. There is good natural pruning for 50 to 60 percent of the bole, even in open-grown trees. Buttresses are small, extending from 0.9 to 3.0 m (3 to 10 ft) upwards from the ground.

The outer bark is greenish brown on young trees, becoming light gray or brown and slightly fissured at maturity. Inner bark is light brown, fibrous, and tasteless. It gives off a slight odor of garlic, a fact that promoted its scientific name *(16)*. Although laurel is native to most of tropical America, it is not yet a major plantation species in the Western or Eastern Hemispheres. Thus, almost all growth records have been collected from trees growing in natural forests. In older, mature stands (more than 80 years), it is common to find only one individual per 2.0 hectares (4.9 acres). In younger stands (less than 30 years), where tolerant species have not yet had time to outgrow laurel, clumps of few to 30 or more individuals can be found over small distances. There are no reports on total longevity.

According to OFI experience with field provenance collections, the best stands of laurel are located on the Caribbean coast of Honduras, Nicaragua, and Costa Rica. The oldest natural stands of laurel for which growth data have been collected are found in the Atlantic lowlands of Costa Rica *(12)*; recorded d.b.h. was 79, 89, and 91 cm (31, 35, and 36 in) for 40-, 50-, and 60-year-old trees. Mean annual growth for an average tree at 40 years was 0.19 m^3 (34 fbm, International 0.25-in Log Scale). A volume table with upper height and d.b.h. limits of 24 m (79 ft) and 76 cm (30 in) exists for laurel found in second-growth forest in Alajuela and Heredia Provinces in northern Costa Rica *(22)*.

Table 1—Height and d.b.h. of laurel *(Cordia alliodora)* in plantations at Los Diamantes and Turrialba, Costa Rica

Plantation location	Age	Total			
		Height		Diameter	
	yr	*m*	*ft*	*cm*	*in*
La Isla *(5)*	29.9	22.0	72.2	25.1	9.9
Los Diamantes *(12)*	24.0	29.3	96.1	37.8	14.9
Bajo Chino (slope) *(5)*	18.4	NA	NA	19.6	7.7
Bajo Chino (flat) *(5)*	18.4	NA	NA	25.4	10.0
Bajo Chino *(5)*	17.0	NA	NA	30.7	12.1
Old Arboretum *(12)*	13.0	13.2	43.3	16.6	6.5
Old Arboretum *(12)*	13.0	19.6	64.3	22.2	8.7
Florencia Norte *(5)*	12.8	NA	NA	18.6	7.3
Old Arboretum *(12)*	10.0	13.4	44.0	21.0	8.3

[1] Not available

Laurel intercrops well with agricultural crops *(40)*. In the coffee region of Chinchina, Colombia, at 1400 m (4,600 ft), in a planting with 100 to 200 laurel trees per hectare (40 to 80/acre), laurel could produce 49 to 74 m^3/ha (700 to 1,057 ft^3/acre) per year over a 20-year period *(26)*. When intercropped with coffee in Costa Rica *(41)*, laurel had a mean annual increment of 10.8 m^3/ha (154 ft^3/acre) in a 15-year-old planting.

Pure plantations of laurel were established as early as 1922 in Nigeria *(30)*. Quantitative growth data are available only from Costa Rica, Puerto Rico, and Surinam. Through age 20 in Costa Rica (table 1), mean annual height and d.b.h. increments were slightly better than 1.0 m (3.3 ft) and 15 mm (0.6 in). Afterwards, growth seemed to decline somewhat. Extrapolating from 7-year data in Surinam, laurel could obtain a minimum outside bark d.b.h. of about 40 cm (16 in) in 25 years *(36)*. Projected d.b.h. growth is 40 to 50 cm (16 to 20 in) at 20 years for plantation sites

Table 2—Height and d.b.h. of laurel *(Cordia alliodora)* on different sites in Puerto Rico

Location	Age	Height		Diameter		Life zone Soils Slope
	yr	*m*	*ft*	*cm*	*in*	
Catalina Nursery	10	17.0	55.8	11.9	4.7	Subtropical Wet, Ultisol, gentle
Luquillo Biosphere Reserve *(38)*						
Tract 10[illegible] *(19)*	6	6.7	22.0	7.1	2.8	Subtropical Moist, Inceptisol, steep
Luquillo Biosphere Reserve	8	7.6	24.9	8.9	3.5	Subtropical Moist, Ultisol, moderate
Toro Negro State Forest *(19)*	8	4.6	15.1	NA[1]	NA	Subtropical Wet, Inceptisol, steep
Carite State Forest *(20)*	9	10.7	35.1	12.7	5.0	Subtropical Wet, Ultisol, gentle
Guilarte State Forest *(20)*	6	3.6	11.8	2.4	0.9	Subtropical Wet, Ultisol, lower slope
Guanica State Forest *(20)*	10	5.0	16.4	9.0	3.5	Subtropical Dry, Alluvium, valley floor

in Colombia *(29)*. In Puerto Rico's young plantations (table 2), height and d.b.h. were better in Subtropical Moist Forests and Subtropical Wet Forests than in Subtropical Dry Forests. But height growth on steep slopes was poorer than height growth on uniform or lower slopes in Subtropical Wet Forests.

Site variation affects laurel growth. In Costa Rica growth was poor on shallow stony soils and on a steep slope having less profile development than an adjacent flat area *(5)*. In Surinam, best diameter growth on sandy soils was on the lower slopes where lower horizons had accumulated sufficient alluvial clay to retain soil moisture during long dry periods *(36)*. On heavier textured soils best growth was also on the lower slopes; texture of the A horizon was lighter (loamy sand) and internal drainage was better there than on the ridge tops where drainage was poor because of plinthite accumulations *(36)*. Observations from Puerto Rico and elsewhere indicate that growth in plantations slows, perhaps considerably, before sawtimber size is reached.

Rooting Habit—No active research on root development is known. Rooting has been reported as deep and extensive in Fiji *(30)* and large and spreading with surface laterals and sometimes a deep taproot in Puerto Rico *(39)*. In both countries laurel has suffered little blowdown or stem breakage in the crowns during cyclonic storms.

Reaction to Competition—Silvicultural research of laurel is still in its infancy. Advances are being made as more countries recognize the value of laurel wood products and the species' potential for fast growth. Any silvicultural technique must consider that laurel is classed as an intolerant pioneer species, demanding lots of light for best growth.

Attempts have been made with limited success to encourage natural regeneration in Costa Rica by mechanically clearing or poisoning undesirable species on selected sites *(5)*. Considerable time and money are needed, however, to keep down weeds or more tolerant shrubs and trees once natural seeding has been established. Other artificial regeneration systems are line and enrichment plantings *(12)*. In line plantings, swaths are cleared through natural forest and laurel seedlings or stump plants are planted at specified spacing up and down the lines. Shade from adjacent forests does not seem to reduce growth of *C. trichotoma* in Argentina *(6)*.

In Surinam, enrichment plantings have been done in two ways *(36)*. In the first, commercial natural forest species are removed and all undesirable plants are poisoned or cut 1 to 2 years before the anticipated planting date. Laurel seedlings are then planted in clumps of three, 1 m (3.3 ft) apart so that each seedling is the apex of an equilateral triangle. Spacing between clumps is 10 by 5 m (33 by 16 ft), or 200 groups per hectare (81/acre). At the final rotation some 130 to 150 trees per hectare (53 to 61/acre) remain. Any laurel natural regeneration is left at planting time.

In the second method used in Surinam, all commercial species with diameters from 20 to 40 cm (8 to 16 in) are left after initial logging of 12.5/ha (30.9/acre) blocks. Rows 250 m (820 ft) long spaced 1.5 m (5 ft) apart are then established in an east-west orientation; planting holes are dug for laurel seedlings at 10 m (33 ft) intervals along the lines. Weeding of seedlings is done by machetes or poisoning. The first thinning is done after 3 years, and the best tree in each group is left.

As early as 1945 in Puerto Rico and 1963 in Costa Rica, laurel was successfully established through the Taungya Method in which tree seedlings are planted between rows of food crops; when crops are harvested the tree seedlings are left in place *(1)*. There are several agroforestry systems under study in Costa Rica now to determine whether laurel can be grown successfully in associations with various cultivated crops *(5)*. Some field observations show that laurel grows better when secondary forest brush is allowed to form the understory than when grass predominates, as occurs in repeatedly cleaned plots *(12)*. The grass may offer greater root competition to laurel trees than the other secondary shrubs.

Damaging Agents—Rodents and birds destroy much of the seed in forest clearings or on direct seeded areas where seeds are not protected or covered *(31)*. Coleoptera of the genus *Amblycerus* also damage laurel seeds *(12)*. In the nursery, seedlings have been infected by a leaf-spot disease in Puerto Rico and by root cutters (*Phyllophaga* spp.) in Venezuela *(12)*. The terminal of outplanted seedlings is very susceptible to damage or malformation from competing weeds and vines *(25)*.

More than 212 different forms of insects were found on laurel in Panama. But none of the seedlings or trees affected showed any signs of serious injury *(12)*. In Puerto Rico laurel foliage has been heavily attacked by the Spanish elm lacewing bug, *Dictyla montropidia (20)*. A canker-causing rust, *Puccinia cordiae*, attacks laurel in the West Indies and has been reported in Guatemala *(12)*. Cankers form at the base of young lateral branches and are sources for usually more serious secondary infections. Trees planted on wet sites are very susceptible. In the Solomon Islands, a black fungal or viral canker (unknown spp.) has caused severe damage to nodes on main stems *(30)*. There may be some relationship between this disease and the fact that these islands are continually humid, with no distinct dry season. Mistletoes (Loranthaceae) are also a problem in some areas *(12)*. At least one grass, *Melinis minutiflora*, has had an adverse effect on laurel growth when extracts from the grass were applied on young seedlings *(12)*. Ant domatia are common in the swollen nodes of laurel lateral branches. They are most prominent in Central America and northwestern South America, being almost totally absent from the West Indies. Ants usually cause no damage to laurel plantings.

Special Uses

Throughout its range, laurel is also used as a shade tree in coffee and cacao plantations as well as in pastures. Humans eat fruits in some places and both seeds and leaves are used for home medicinal purposes *(15)*. Laurel is suitable for ornamental use in urban residential areas and has been tried for use in honey production because of its copious flowering *(16)*. In Brazil it yielded 266 liters (70 gal) of ethanol per ton of dry material; this compares well with a yield of 325 liters (86 gal) per ton produced by *Protium* spp., the best of 25 species tested *(28)*.

Laurel is still to be evaluated fully for pulping; physical and mechanical properties of sawn and roundwood are quite good. General strength properties are good and similar to those of mahogany *(4,9,34)*. Specific gravity ranges from 0.44 to 0.52 *(10)*. Freshly felled material seasons rapidly with only slight warping and checking; volumetric shrinkage is around 9 percent. Wood is easy to work, finishes smoothly, and glues readily *(18)*. Heartwood is not receptive to preservative treatments but has some resistance to fungi, termites, and marine borers *(4)*. Degree of resistance appears to be related to coloring of the heartwood, darker colored wood being more resistant than lighter colored heartwood. Heartwood coloring is also used to distinguish between laurel blanco (light) and laurel negro (dark) wood in Central America *(27)*. The former is associated with the soft-wooded *Cordias*, like *C. alliodora*; the latter is associated with the harder, heavier density (specific gravity 0.63 to 0.84) *Cordias* like *C. gerascanthus (4)*. Variations in heartwood coloring within any of two major groups could be caused by local site properties as well as by age *(27)*.

Genetics

Considerable confusion still exists as to the taxonomy of laurel. Great variation in climate, soils, and elevation within its extensive natural range contribute to large differences in flowering and fruiting phenology and morphological features such as flower and leaf size *(30)*. Thus *Cordia alliodora* has several botanical synonyms. The most common are *Cerdana alliodora* and *Cordia gerascanthus*. There is some doubt whether *Cordia trichotoma*, growing in Brazil and Argentina, is really a separate species or merely a variety of *C. alliodora (30)*.

Two distinct races are recognized in Costa Rica and probably exist throughout the extensive native range which includes wet and dry habitats *(12)*. Laurel was included in the 1977 FAO Panel of Experts Report on Forest Genetic Resources Priorities for Mexico, the Caribbean, and Central and South America *(8)*. The species is not in danger of disappearing because of its large range, but there are areas, such as in Colombia, where overcutting may destroy local populations. For this reason and the fact that the species exhibits fast growth in plantations and has utility for various wood products, there is an urgent need for botanical, genecological, and collecting work.

The most vigorous collection program for provenance testing now underway is that coordinated by the OFI. Since 1977, 19 native and 2 exotic collections have been made, within altitudinal ranges of 50 to 2000 m (160 to 6,600 ft) and precipitation ranges of 1040 to 4700 mm (41 to 185 in). Most results have been analyzed for trials only 1 year old. Definite trends are not yet possible to interpret but the Finca la Pineda, Nicaragua, seed source has consistently performed well, as have the Finca la Fortuna and San Francisco sources from the north coast of Honduras. Sources from Costa Rica have usually given rather poor nursery results but surviving trees have performed well in the field *(30)*. A separate collection of 24 Costa Rican plus-trees did poorly in Puerto Rico from 1976 to 1978 and the test was closed after 2 years *(42)*. Tree improvement work is also underway with laurel in Colombia; 31 superior trees were selected in 1978 *(35)*. Seed collection areas have also been designated in Costa Rica and Colombia *(29)*. As the OFI-coordinated trials develop and more data are analyzed, interesting trends should become discernible as to adaptation of laurel provenances to particular soil, climate, and altitudinal regions.

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Cornus florida L. Flowering Dogwood

Cornaceae Dogwood family

B. F. McLemore

Flowering dogwood *(Cornus florida)* is one of America's most popular ornamental trees. Known to most people simply as dogwood, it has other common names, including boxwood and cornel. The species name *florida* is Latin for flowering, but the showy petal-like bracts are not in fact flowers. The bright red fruit of this fast-growing short-lived tree are poisonous to humans but provide a great variety of wildlife with food. The wood is smooth, hard and close-textured and now used for specialty products.

Habitat

Native Range

The range of flowering dogwood (figs. 1, 2) extends from extreme southwestern Maine west to New York, extreme southern Ontario, central Michigan, central Illinois, and central Missouri; south to extreme southeast Kansas, eastern Oklahoma, east Texas; and east to north Florida. A variety also grows in the mountains of Nuevo León and Veracruz, Mexico *(11)*.

Climate

Precipitation within the range of flowering dogwood varies from 760 mm (30 in) in the North to 2030 mm (80 in) in the southern Appalachians. Warm season precipitation varies from about 510 mm (20 in) in southern Michigan to 860 mm (34 in) in northern Florida, and annual snowfall ranges from none in Florida to more than 127 cm (50 in) in the North *(15)*. Average annual temperature is 21° C (70° F) in the South and 7° C (45° F) in the North, with temperature extremes of 46° to –34° C (115° to –30° F). Growing season ranges from 160 days in southern Michigan to more than 300 days in Florida *(12)*.

Soils and Topography

The species grows on soils varying from deep and moist along minor streams to light textured and well drained in the uplands. It is found most frequently on soils with a pH of 6 to 7 *(15)*. Dominant soil orders (with typical suborders in parentheses) in the range of flowering dogwood, in decreasing order of importance, include Ultisols (Udults and Aquults) in the South and East, Inceptisols (Ochrepts) in the Appalachians, Alfisols (Udalfs) in the Midwest, Spodosols (Orthods and Aquods) in New England and Florida, and Entisols (Psamments) in scattered areas of the Southeast *(14)*. Seedling survival is low and the species is virtually absent on poorly drained clay soils. The frequency of flowering dogwood in forest stands increases as drainage improves and soils become lighter in texture.

Flowering dogwood grows well on flats and on lower or middle slopes, but not very well on upper slopes and ridges. The inability to grow on extremely dry sites is attributed to its relatively shallow root system. It is one of the most numerous species in the understory of loblolly pine and loblolly pine-hardwood stands in the South. As these stands progress toward the hardwood climax, dogwood remains an important subordinate species.

Flowering dogwood is considered a soil improver *(7)*. Its leaf litter decomposes more rapidly than that of most other species, thus making its mineral constituents more readily available. Dogwood foliage decomposes three times faster than hickory *(Carya* spp.); four times faster than yellow-poplar *(Liriodendron tulipifera)*, eastern redcedar *(Juniperus virginiana)*, and white ash *(Fraxinus americana)*; and 10 times faster than sycamore *(Platanus occidentalis)* and oak *(Quercus* spp.) *(15)*. In addition to its rapid decomposition, dogwood litter is an important source of calcium, containing 2.0 to 3.5 percent of this element on an oven-dry basis. The range of major mineral elements, in milligrams per kilogram of foliage (parts per million), is as follows: potassium, 4,000 to 11,000; phosphorus, 1,800 to 3,200; calcium, 27,000 to 42,000; magnesium, 3,000 to 5,000; and sulfur, 3,800 to 7,000. The range of minor elements, in mg/kg (p/m), is boron, 23; copper, 7 to 9; iron, 240 to 380; manganese, 30 to 50; and zinc, 3 to 28 *(15)*.

Dogwood leaves concentrate fluorine and may contain 40 mg/kg (p/m) compared to only 8 mg/kg (p/m) for apple *(Malus* spp.) and peach *(Prunus* spp.) leaves grown under similar conditions. In one study, fluorine increased from 72 mg/kg (p/m) in June to 103 mg/kg (p/m) in October, while that of black cherry *(Prunus serotina)* increased from 5.6 to 11.3 mg/kg (p/m) *(15)*.

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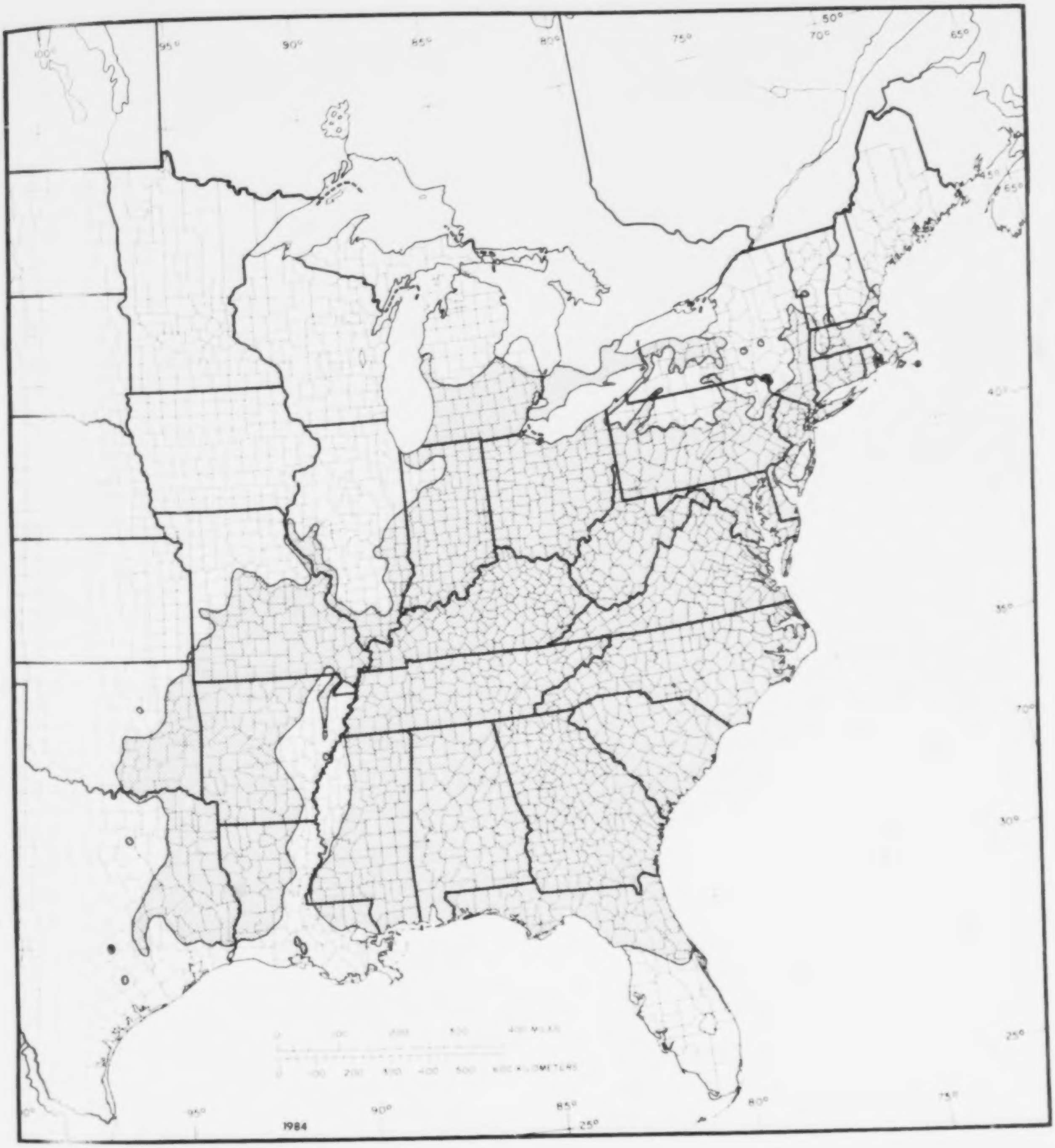
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Figure 1—*The native range of flowering dogwood.*

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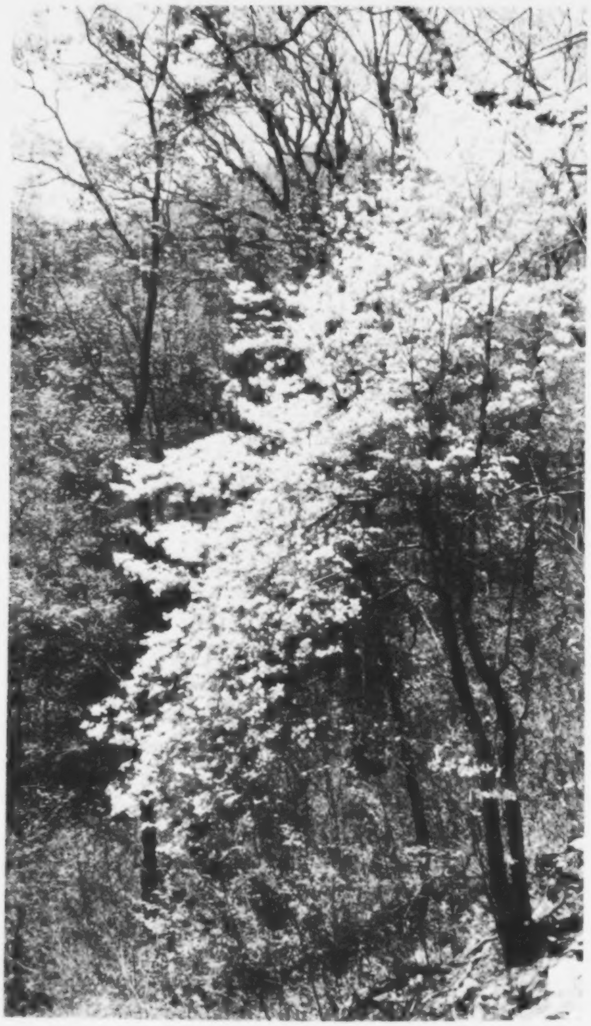

Figure 2—*Flowering dogwood.*

Associated Forest Cover

The wide geographical range of flowering dogwood, and the diverse soils on which it is found, is indicative of a large number of associated species. Dogwood is specifically mentioned in 22 of the 90 Society of American Foresters forest cover types *(3)*. Cover types range from Jack Pine (Type 1) and Beech-Sugar Maple (Type 60) in the North to Longleaf Pine (Type 70) in the South. Common associates include white, red, and black oaks *(Quercus alba, Q. falcata, Q. velutina)*, yellow-poplar, sassafras *(Sassafras albidum)*, persimmon *(Diospyros virginiana)*, sweetgum *(Liquidambar styraciflua)*, and longleaf, loblolly, shortleaf, slash, and Virginia pines *(Pinus palustris, P. taeda, P. echinata, P. elliottii,* and *P. virginiana)*. A complete list of species found with dogwood would include a majority of the trees growing in the Eastern United States.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowering dogwood has many crowded, small, yellowish perfect flowers, borne in terminal clusters in the spring before the leaves appear, and surrounded by four snow-white, petal-like bracts. The bracts form "flowers" 5 to 10 cm (2 to 4 in) across and provide a spectacular display in the springtime. Occasionally, trees with salmon-colored or light-pink bracts are found in nature. Pink and red flowering dogwoods and other cultivars with special ornamental characteristics are commonly propagated from clones by commercial nurseries. Dates of flowering range from mid-March in the South to late May in the North.

The clustered fruits of flowering dogwood are bright red drupes about 13 mm (0.5 in) long and 6 mm (0.25 in) in diameter with thin, mealy flesh. Each fruit contains a two-celled, usually two-seeded, bony stone. In many stones, only one seed is fully developed. The fruits ripen from September to late October *(10)*. Trees grown from seed commonly flower and produce fruits when 6 years old. Flowers also have been observed on trees of sprout origin at 6 years, when stump diameter is 19 mm (0.75 in), and height is 1.2 m (4 ft).

Seed Production and Dissemination—Dogwood usually produces a good seed crop every other year, but seeds on isolated trees are frequently empty. Thus, seed collections should be made from groups of trees. In a Texas study, 88 percent or more of trees 9 cm (3.4 in) in d.b.h. and larger bore fruit each year. Year-to-year differences were more pronounced in the smaller diameter classes. Average fruit production was 185 kg/m^2 of basal area (37.9 lb/ft^2) *(9)*.

The yield of stones per kilogram of fruit ranges from 0.19 to 0.46 kg (19 to 46 lb/100 lb of fruit). The average number of cleaned stones per kilogram is 9,920 (4,500/lb). Clean, air-dried stones may be stored in sealed containers at 3° C (38° F) for 2 to 4 years *(2)*. Birds and other animals are the primary agents of seed dissemination, although some seeds are scattered by gravity.

Seedling Development—Natural germination of flowering dogwood usually occurs in the spring following seedfall, but some seeds do not germinate until the second spring. Germination is epigeal. Stratification of freshly collected seed at 5° C (41° F) for periods up to 120 days is recommended for overcoming embryo dormancy *(2)*.

Seedlings usually show rapid root growth. In one greenhouse study, an average 6-month-old seedling had 3,000 roots with a total length of 51.2 m (168 ft), compared to 800 roots with a total length of 3.7 m (12 ft) for loblolly pine *(15)*.

This species grows nearly all summer but stops temporarily during periods of adverse conditions. In a Massachusetts nursery, flowering dogwood displayed a height growth pattern different from that of any other species studied. Seedlings grew from April 24 to September 4, and 90 percent of the growth occurred from May 15 to August 18. The most rapid growth occurred during the first week of August *(10)*.

In a North Carolina Piedmont study, flowering dogwood seedlings were planted under three situations: (1) in an open field, (2) under pine stands, and (3) on the margins of pine stands. Survival was significantly higher on the margins of pine stands than on the other two sites, but there was no significant difference in survival between the open field and the pine forest. The intermediate light intensity of the margins apparently provided some advantage. Growth of seedlings was greater in the open than on the margin of the pine forest. Seedlings in the forest were smallest *(15)*.

Transplanting flowering dogwood seedlings with a root ball is preferred over bare-root transplanting, although both methods can be successful *(4)*. Plants entering their third year are well suited for planting in permanent locations. Plants of this age are usually 0.6 to 1 m (2 to 3 ft) tall and can be lifted easily without excessive disturbance of the root system.

Vegetative Reproduction—Flowering dogwood reproduces by sprouting and sprouts most profusely when cut in late winter. Height growth of sprouts is known to increase with increasing stump diameter. The species also reproduces extensively by layering. Other means of vegetative propagation include softwood cuttings in summer, hardwood cuttings in winter, grafting in winter or spring, suckers and divisions in spring, and budding in the summer. Vegetative reproduction is necessary to propagate plants for characteristics such as fruit retention and color of bracts and fruit.

Flowering dogwood roots readily from cuttings taken in June or immediately after the plants bloom. Cuttings from young trees usually show better growth and survival after rooting than cuttings from mature trees. Only terminal shoot tips trimmed to about 8 cm (3 in) in length and retaining two to four leaves should be used. Bases of cuttings should be dipped in a mixture of indolebutyric acid crystals and talc, one part acid crystals to 250 parts talc by weight *(10)*. Cuttings are then set about 3 cm (1.2 in) deep in the rooting medium and grown under a mist with a photoperiod of at least 18 hours.

The red form of flowering dogwood is difficult to start from cuttings and usually is propagated by budding in late summer or grafting in winter *(6)*.

Sapling and Pole Stages to Maturity

Growth and Yield—The maximum size obtained by a flowering dogwood is 16.8 m (55 ft) in height and 48 cm (19 in) in d.b.h. as recorded in the American Forestry Association's register of champion trees. Heights on good sites of 9 to 12 m (30 to 40 ft) are common, with ranges in d.b.h. of 20 to 40 cm (8 to 16 in). On poorer sites, d.b.h. of mature trees may range from only 8 to 20 cm (3 to 8 in). Near the northern limits of its range, dogwood is a many-branched shrub *(15)*. Height growth in the southern Appalachians is reported to be fairly rapid for the first 20 to 30 years, but then it practically ceases. Individual plants may live for 125 years. Annual growth rings are usually 2 to 4 mm (0.06 to 0.15 in) wide *(12)*.

Flowering dogwood seldom if ever grows in pure stands. Thus, because it is usually a small, understory tree, little or no information is available concerning growth and yield on a per-acre basis. Moreover, it is treated as a weed tree in timber stand improvement operations more often than it is grown for its commercial value. One estimate has indicated that yields of 12.6 m^3/ha of boltwood (2 cords/acre) may be cut on good sites, but it takes 15 to 20 times the area to obtain half this amount in other locations *(15)*. No estimates of the volume of flowering dogwood are available for the entire range of the species. One writer noted that in six Southern States, where production is concentrated, a volume of 2.82 million m^3 (99.8 million ft^3) in trees 12.7 cm (5 in) d.b.h. and larger was shown by inventories made between 1962 and 1971 *(12)*. This indicates a supply of more than 2.55 million m^3 (1 million cords) within the six States.

Rooting Habit—The extensive root system of flowering dogwood is extremely shallow. This fact undoubtedly accounts for the susceptibility of this species to periods of drought.

Reaction to Competition—Flowering dogwood is an understory species and is classed as very tolerant of shade. Maximum photosynthesis occurs at slightly less than one-third of full sunlight *(15)*. It is tolerant of high temperatures. Soil moisture usually is the limiting factor. In Southern forests, dogwood leaves are often the first to wilt in dry weather. Continuing drought may cause leaves to fall and dieback of tops to occur.

Damaging Agents—Because of its thin bark, flowering dogwood is readily injured by fire. Its profuse sprouting ability may actually increase the number of stems in fire-damaged stands, however *(12)*. Flooding also is detrimental to flowering dogwood.

Little is known of the pest status of insects associated with wild flowering dogwoods, but many insects have been identified attacking cultivated ornamentals. The dogwood borer *(Synanthedon scitula)* is a noteworthy pest of cultivated flowering dogwood. Other damaging insects include flatheaded borers *(Chrysobothris azurea* and *Agrilus cephalicus)*, dogwood twig borer *(Oberea tripunctata)*, the twig girdler *(Oncideres cingulata)*, scurfy scale *(Chionaspis lintneri)*, and dogwood scale *(C. corni) (1)*. Dogwood club gall, a clublike swelling on small twigs, is caused by infestations of midge larvae *(Resseliella clavula)* and is a serious problem in some areas *(10)*. The redhumped caterpillar *(Schizura concinna)*, a tussock moth *(Dasychira basiflava)*, io moth *(Automeris io)*, and scarab beetles *(Phyllophaga* spp.) are among the numerous leaf feeders attacking dogwood *(1)*. Introduced pests of flowering dogwood include the Japanese weevil *(Pseudocneorhinus bifasciatus)* and Asiatic oak weevil *(Crytepistomus castaneus) (8)*.

Basal stem canker, caused by the fungus *Phytophthora cactorum*, may girdle the tree and is the most lethal disease. Target cankers *(Nectria galligena)* sometimes occur on the trunk and limbs, and *Armillaria mellea* has been found on dogwoods. Leafspot *(Cercospora cornicola)* attacks seedlings, and *Meliodogyne incognita* causes severe root galling, associated with dieback and premature leaf fall in seedlings. Twig blight, caused by the fungus *Myxosporium nitidum*, may cause dieback of small twigs. Leaf spots and dieback of flowers are caused by *Botrytis cinerea, Elsinoe corni,* and *Septoria cornicola*, while *Ascochyta cornicola* may result in shrivelling and blackening of the leaves *(7)*. Verticillium wilt *(Verticillium albo-atrum)* attacks dogwood *(15)*, and the cherry leafroll, tobacco ringspot, and tomato ringspot viruses have been isolated from dogwood leaves *(13)*.

Noninfectious diseases include sunscald, mechanical and drought injury, and freezing. Dogwood reproduction is often browsed heavily by deer and rabbits.

Special Uses

Flowering dogwoods are extremely valuable for wildlife because the seed, fruit, flowers, twigs, bark, and leaves are utilized as food by various animals. The most distinguishing quality of dogwood is its high calcium and fat content *(5)*. Fruits have been recorded as food eaten by at least 36 species of birds, including ruffed grouse, bob-white quail, and wild turkey. Chipmunks, foxes, skunks, rabbits, deer, beaver, black bears, and squirrels, in addition to other mammals, also eat dogwood fruits. Foliage and twigs are browsed heavily by deer and rabbits. The quality of browse may be improved by controlled burns in the spring, which increase the protein and phosphoric acid content.

Flowering dogwood also is a favored ornamental species. It is highly regarded for landscaping and urban forestry purposes.

Virtually all the dogwood harvested was used in the manufacture of shuttles for textile weaving, but plastic shuttles have rapidly replaced this use. Small amounts of dogwood are used for other articles requiring a hard, close-textured, smooth wood capable of withstanding rough use. Examples are spools, small pulleys, malletheads, jewelers' blocks, and turnpins for shaping the ends of lead pipes *(12)*.

Genetics

Near the northern limits of its range, flowering dogwood becomes a many-branched shrub *(15)*. Other than this, little is known of population differences other than the tendency for fruit weights to decrease with decreasing latitude and increasing length of growing season *(16)*.

More than 20 cultivars of flowering dogwood are sold commercially in the United States *(17)*. Four clones of flowering dogwood most commonly propagated as ornamentals are *Cornus florida* f. *pendula* (Dipp.) Schelle, with pendulous branches, *Cornus florida* f. *rubra* (West.) Schelle, with red or pink involucral bracts, *Cornus florida* f. *pluribracteata* Rehder, with six to eight large and several small bracts on the inflorescence, and *Cornus fl*[illegible] *xanthocarpa* Rehder, with yellow fruit. A [illegible] cultivar, called *Welchii*, has yellow and [illegible] variegated leaves and is offered commercially [illegible].

In addition to these clones, *Cornus florida* var. *urbaniana*, a variety found in the mountains of Nuevo León and Veracruz, Mexico, differs from the typical species by its grayer twigs and larger fruit *(15)*.

Flowering dogwood is not known to hybridize with other species.

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Dacryodes excelsa Vahl   Tabonuco

Burseraceae   Bursera family

Ariel E. Lugo and Frank H. Wadsworth

Tabonuco (*Dacryodes excelsa*), also known as gommier and candlewood, is the dominant large tree of the native forests that formerly covered the northern lower and middle slopes of the mountains of Puerto Rico. It is distinguished by broad low buttresses, a columnar bole, smooth gray bark, and pinnately compound leaves with five to seven fragrant, dark-green leaflets. When wounded, the tree exudes a clear, fragrant inflammable resin that hardens and turns white on exposure.

Habitat

Native Range

Tabonuco (fig. 1) is native to elevations from 200 to 900 m (660 to 2,800 ft) throughout Puerto Rico. On favorable sites, it may make up 35 percent of the basal area and 80 percent of the timber volume of the forest, commonly termed *Dacryodes—Sloanea* association *(1)*. From Puerto Rico, the native range of tabonuco extends into the Lesser Antilles on St. Kitts, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, and Grenada, a gross forest area of about 2300 km^2 (888 mi^2) *(24)*. Other members of the genus are in South America and Africa *(5,8)*.

Climate

Tabonuco in Puerto Rico is found within a mean temperature range of 21° to 25° C (70° to 77° F) and a mean annual precipitation range from 2000 to 4000 mm (79 to 157 in). Precipitation is generally abundant except from February through April, when it may drop to about 75 mm (3 in) per month. At El Verde, on the northwestern slope of the Sierra de Luquillo at an elevation of 420 m (1,380 ft), well within the tabonuco forest range, data collected over 3 years showed the following: mean temperature, 22.6° C (73° F); mean absolute humidity, 18.7 g/m^3 (0.02 oz/ft^3); mean relative humidity, 91 percent; mean daily insolation, 383 gcal/cm^2 (383 ly) mean daily pan evaporation, 1.8 mm (0.07 in); mean wind velocity, 4.2 km/h (2.6 mi/h); and mean annual rainfall, 3700 mm (146 in). Diurnal variations are smaller than some seasonal changes *(16)*.

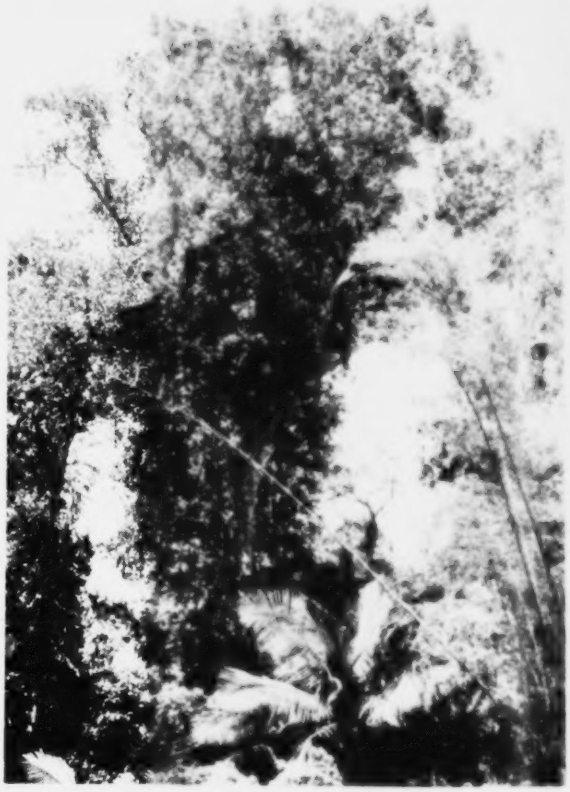

Figure 1—*A mature tabonuco showing spreading crown.*

Soils and Topography

Tabonuco grows on deep, red, acid (pH 4.5 to 5.5), clay soils (Ultisols such as Los Guineos and Humatas) derived from igneous rock. Typically these soils are stony, often with large boulders, and internal drainage is good. Large tabonuco trees tend to be concentrated on upper slopes and ridges, where they may form nearly pure groups whose roots are grafted, thus forming a tree union or clumps of trees. Presumably this reflects the better drainage of soils at such locations or the superior anchorage against hurricane winds that the prominent boulders may offer. Significantly superior diameter growth rates of

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tabonuco on ridges as compared to swales have been reported *(22)*.

Associated Forest Cover

Tabonuco dominates a forest association known locally as the tabonuco type *(21)*. In the French West Indies, the association is described as "forest hygrophytique" *(20)*, and Beard described it as lower montane rain forest, or *Dacryodes-Sloanea (1)*. These fall within the broader categories of Tropical or Subtropical Wet Forest life zones *(7)*.

In Puerto Rico this association averages about 50 tree species per hectare (50/2.5 acres) larger than 10 cm (3.9 in) in d.b.h. In the Luquillo Mountains close associates include motillo *(Sloanea berteriana)*, palma de sierra *(Prestoea montana)*, yagrumo hembra *(Cecropia peltata)*, yagrumo macho *(Didymopanax morototoni)*, and caimitillo verde *(Micropholis garcinifolia) (21)*. The forest type has been described in detail *(2,15,21)*. Characteristics of tabonuco stands include a rich mix of 170 tree species in primary and secondary stands *(23)* with dominants of *Sloanea berteriana*, *Guarea guidonia*, and *Manilkara bidentata*. The relative density of seedlings to that of canopy trees approximates a ratio of 8 while that of saplings is 0.4 *(19)*. On the average, the stand contains 116 trees per hectare (47/acre) 10 to 15 cm (3.9 to 5.9 in) in d.b.h., 100 to 150/ha (40 to 61/acre) larger than 30 cm (11.8 in) in d.b.h., and 63/ha (25/acre) larger than 50 cm (19.7 in) in d.b.h. with a total biomass of 424 t/ha (156 tons/acre) of which 33 percent is in tree boles *(14,23)*. The basal area of the average stand approximates 40 to 46 m^2/ha (174 to 200 ft^2/acre) and the volume approximates 300 to 345 m^3/ha (4,285 to 4,930 ft^3/acre) *(2)*. The diurnal gross primary production of a stand with a leaf area index of 6 to 7 in Puerto Rico is reported to average 16 grams of carbon per square meter of ground area (0.052 oz/ft^2) *(14)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Male and female flowers appear on different trees, making this a dioecious species. Flowers are greenish, about 4 mm (0.16 in) across, and develop in lateral, much-branched panicles. The fruit, a one-seeded oblong-ovoid drupe about 19 mm (0.75 in) in diameter, has a corrugated surface when dry *(19)*. The seed is fleshy, with folded cotyledons *(5,17)*.

Flowering peaks between May and November, with most fruit falling from October to December. There is some flowering and fruiting at other times and considerable annual variation. Empty fruits commonly fall earlier than those that are fertile. At one period during the autumn of 1963, two-thirds of the crop was composed of empty fruits, although a second smaller crop of viable seeds appeared later. Gamma radiation stress reportedly has led to earlier and increased fruit fall *(6)*. Fruits are generally found in abundance beneath the crowns of the parent trees.

Seed Production and Dissemination—Of the fruits that fall, those dark in color were found to be heavier, with 60 fruits per kilogram (27/lb) compared to 73 per kilogram (33/lb), and more viable, up to 22 percent compared to up to 5 percent, than green fruits. Completely developed fruits tend to sink when immersed in water. Of those that float, most are hollow, although as many as 33 percent may still be viable. The period of viability under natural conditions is short but not precisely known. A few seeds are known to have survived 5 weeks storage exposed to the air.

Germination is epigeal and takes place within a few days under humid, shady conditions. Under direct exposure to the sun, germination is less than in the shade, 11 percent compared to 28 percent in one test.

Seedling Development—In nature the seedlings grow best on steep slopes under low light intensities (0.07 to 0.05 gcal/cm^2. min or 0.07 to 0.05 ly). They are fragile and root within the litter layer. At an age of 4 months they attain an average height of 16 cm (6.3 in) and typically have six leaves. In some areas there may be as many as four seedlings per square meter (0.4/ft^2). Few seedlings grow beyond this stage, only half surviving beyond 8 months. Continued growth of the remaining seedlings under intermediate light intensities is slow. Net photosynthesis is low (60 mg of carbon per m^2.h or 0.08 gr/ft^2.h), and the ratio of net photosynthesis to respiration is 0.78 *(12)*.

In the nursery it has been found that seedlings during their first month will not withstand direct exposure to the sun. Under shady conditions seedlings attained 22 cm (8.7 in) in 6 months. Like many other large-seeded tree species, tabonuco does not survive bare root transplanting. In contrast, 85 percent survival has been attained by the use of containers with an intact ball of earth about the roots. At 9 years, trees were 3.0 to 4.3 m (10 to 14 ft) in height and 3.8 to 5.0 cm (1.5 to 2.0 in) in d.b.h. *(13)*.

Direct sowing in the forest has yielded germination as high as 33 percent but subsequent problems such as leaf fall, drought, and vines precluded successful establishment, so planting is recommended.

Vegetative Reproduction—There is no evidence of vegetative reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature tabonucos in Puerto Rico may reach 35 m (115 ft) in total height and 180 cm (71 in) in d.b.h. The age of large trees is estimated at up to 400 years. Unpublished preliminary volume tables exist for the species, and a composite table for tabonuco type forest has been published *(2)*. Because of the mixed nature of the forests in which tabonuco is found, growth and yield of tabonuco per unit of forest area are somewhat meaningless.

Diameter growth of individual trees is most rapid on slopes and unexposed ridges and for specimens that are large in size and dominant in crown position (0.15 cm/yr, 0.06 in/yr, for dominant crowns in mature stands vs 0.10 cm/yr, 0.04 in/yr, for suppressed crowns). Growth rates are slow when compared to planted exotics, but what the potential growth of tabonucos would be if planted under comparable conditions is not known.

Rooting Habit—The observed preference of tabonuco for upper slopes and ridges and its obvious successful survival of frequent hurricane winds that break crowns rather than uprooting trees point to a strong and presumably deep root system. Root grafts among trees of this species are common and can be seen in stumps that remain alive and continue to develop callus over the cut surface for decades. Anywhere from 10 to 20 individual trees can form a union as a result of root grafts. Dense and deep root-mats develop near the bases of some large trees, presumably where unusually large amounts of litter are trapped on the surface.

Reaction to Competition—Overall, tabonuco may be classed as intermediate in tolerance to shade. Seedlings are very tolerant. Only a tiny proportion of the seeds that fall produce trees that reach maturity. Competitive factors include light, moisture, mechanical damage resulting from the falling of litter or other trees, and smothering by vines. For best survival, seedlings need to be free of competition until they are at least 3 or 4 m (9.8 to 13 ft) tall.

Growth rates of established trees can be accelerated if the trees are released from competition (i.e., from 0.15 cm/yr, 0.06 in/yr, in mature stands to 0.66 cm/yr, 0.26 in/yr, in cutover stands). However, even mature trees will suffer shock if severely exposed to the intensive rays of the sun, due in part to scalding of previously shaded bark. Trees severely isolated in residual stands after logging have been observed to exhibit crown deterioration and will be lost within 10 years.

Damaging Agents—The success of tabonuco in the mountains of the West Indies speaks for its capability for dealing with hurricanes. Many trees do not survive, and many of those that do, suffer crown breakage and subsequent heart rot. Despite this, most of the mature trees in Puerto Rico have sound butt logs. A few trees exhibit bark swelling and cankers that provoke an abundance of resin exudation. The pathogen is unknown. Abortion of the fruits is a common and possibly an important phenomenon whose causes are unknown. The significance of fertile seed removal by parrots, other vertebrates, and invertebrates is not known either.

Special Uses

Tabonuco wood is used for all types of furniture, cabinet work, interior trim, general construction, and carpentry. The wood is also useful for crates, boxes, shingles, and small boats. It is a substitute for mahogany in a variety of uses. The wood itself is moderately heavy, with a specific gravity of 0.53 *(19)*. It air-seasons easily and satisfactorily, undergoes moderate and uniform shrinkage during seasoning, and holds its place well after manufacture. Tabonuco is a moderately good machining wood; it cuts and saws easily but will dull saw teeth due to its high silica content. Tabonuco lumber yields good surfaces when planed, sanded, mortised, or shaped (turning and boring are more difficult). It is easily glued, holds nails well, takes stain well, and finishes beautifully with varnish or lacquer. The wood is only slightly resistant to decay, lasting 3 years or less in the ground, and is difficult to impregnate with preservatives by either pressure or nonpressure methods *(11,12,18)*. Tabonuco wood compares favorably with mahogany and birch *(24)*.

Early settlers used the resin of tabonuco for making candles and torches, for caulking boats, for incense, and for medicinal purposes. The endangered Puerto Rican parrot feeds on tabonuco seeds.

Genetics

Wood cutters in Puerto Rico have recognized two races of tabonuco based on the degree of red color and other visible properties of the wood. Other variations, such as the shape of the fruit, have been observed. The genetic significance of these traits, if any, is unknown. *Dacryodes excelsa* has a nuclear volume of 52.6 μ^3 *(9)* and shade leaves appear to contain less DNA than sun leaves, 590 compared to 715 Mg/g *(3)*.

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Didymopanax morototoni (Aubl.) Decne. & Planch.
Yagrumo Macho

Araliaceae **Ginseng family**

L. H. Liegel

Yagrumo macho (*Didymopanax morototoni*) is a well-known pioneer species throughout the tropical Americas. In commerce, the common name is morototo or matchwood because the wood is used for match splints in several countries. The light weight wood is also substituted for certain grades of balsa.

Habitat

Native Range

Yagrumo macho is the most widely distributed species within the genus *Didymopanax*. The range is extensive, roughly from latitude 17° N. to 25° S., and covers wet and moist forests of the West Indies, from Cuba to Trinidad, and continental tropical America from the States of Oaxaca and Veracruz in Mexico, through Colombia, Venezuela, the Guianas, Brazil, and Argentina (*4,12,15,23,25,26,33*). The species was introduced to Jamaica and has been planted in southern Florida. In Puerto Rico it is quite common, growing in over half of the municipalities and in 8 of 13 State Forests, but it is not common anywhere else in its range. In Panama it is reportedly more abundant on the Pacific side than on the Atlantic side. Local or regional range maps are known only for Colombia and Puerto Rico (*13,16,28*).

Climate

In Puerto Rico yagrumo macho grows in Subtropical Moist, Subtropical Wet, and Subtropical Rain Forest life zones (*10*). Mean annual temperatures in these life zones range from 24° to 26° C (75° to 79° F), 22° to 24° C (72° to 75° F), and 22° to 23° C (72° to 73° F) with mean annual precipitation of roughly 1500, 3000, and 4000 mm (60, 120, and 160 in), respectively. Elsewhere, yagrumo macho grows in similar life zones, and mean annual precipitation may exceed 5000 mm (200 in) in some parts of the range, as in Colombia (*28*).

Soils and Topography

Yagrumo macho is not exacting in soil requirements. Therefore, it grows well on a variety of soils, especially those that have been abandoned after agricultural use. In Trinidad, stands are found on flat areas having deep, bleached sands (Entisols) and on gently undulating areas having outcrops of acidic clays (Ultisols or Inceptisols) (*2,19*). In Puerto Rico the species grows most commonly on either deep or shallow acid clays (Ultisols and Inceptisols) in the mountains or on calcareous soils (Mollisols) in the "haystack" (mogote) limestone hills.

Although yagrumo macho grows on flat areas in Puerto Rico, particularly near streams, it is more predominant in upland dissected terrain (*17*) from 100 to 900 m (330 to 2,950 ft); slopes are usually 45 percent or more. On the western end of Puerto Rico, it grows almost at sea level (*21*). The highest elevations reported for yagrumo macho are in Colombia, where it can be found from 500 to 1700 m (1,640 to 5,580 ft) (*28*).

Associated Forest Cover

Throughout its range yagrumo macho is a common species in secondary forests, in natural or man-made openings in mature forests, or along roadsides and river banks. In Puerto Rico's Subtropical Wet Forest it is often associated with yagrumo hembra or trumpet-tree (*Cecropia peltata*) and guano or balsa (*Ochroma pyramidale*), which are also fast-growing, large-leafed successional species having similar physiognomies (*10*). In openings caused by blowdowns it is also associated with tabonuco (*Dacryodes excelsa*), the mature component in natural remnants of the Subtropical Wet Forest in Puerto Rico.

In the State of Oaxaca, Mexico, yagrumo macho grows with other thicket species like pegoge (*Tabernaemontana arborea*), mata-raton (*Gliricidia sepium*), *Vernonia patens*, *Acacia globulifera*, camasey (*Miconia* spp.), *Belotia cambellii*, and cerezo (*Cordia glabra*) (*32*). Three locally important and associated hardwood species in Trinidad are gommier (*Protea insigne*), *Sterculia caribaea*, and serette (*Byrsonima spicata*) (*2*). In Venezuela yagrumo macho and yagrumo hembra form a transition zone between guaba (*Inga* spp.) stands growing along the rivers and high forest stands of *Parkia pendula* occurring

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further inland *(34)*. In the Bajo Atrato region of Colombia it is associated with *Simarouba* spp., boxwood (*Jacaranda copaia*), and *Schizolobium parahybum (20,22)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yagrumo macho has perfect flowers and reproduces in a yearly cycle. Of 96 trees observed for 14 months between 1976 and 1977 in the Luquillo Mountains and at the Rio Piedras Agricultural Experiment Station in Puerto Rico, 58 flowered mainly from October through December *(21)*. There was significantly less flowering in other months. Minimum sizes of trees producing fruits were 6.4 m (21 ft) tall and 10.2 cm (4 in) in d.b.h. In Trinidad, flowers have been observed mainly in October but also in April and September *(19)*. Information on flowering in other countries is not available, but with yagrumo macho's rather extended range, great latitudinal variation in flowering and fruiting can be expected. Flowers are numerous and grouped at ends of branches into many rounded clusters, from 0.3 to 0.6 m (1 to 2 ft) long. The 5-petaled, fine brownish and gray hairy flowers are about 5.0 mm (0.2 in) across, with white petals about 1.5 mm (0.06 in) long, and five stamens and two styles *(16,21)*.

Pollination mechanisms have not been studied in detail. Bees of the *Trigona* and *Mellipona* genera have been observed on yagrumo macho flowers in Costa Rica. Ants of the *Crematogaster* genus may also play a role.

It takes approximately 1 to 2 months for flowers to develop into fruits. Immature fruits are dark green or deep purple. They are fleshy, 4 to 6 mm (0.16 to 0.24 in) long, 7 to 10 mm (0.28 to 0.39 in) wide, and about 2 mm (0.08 in) thick. Fruits usually contain two and occasionally three oblong and flattened brown seeds, about 5 mm (0.2 in) long. Mature fruits are dropped almost every month in Puerto Rico, but production peaks from November through June *(21)*. In Costa Rica fruits mature in January and fall from February through May.

Seed Production and Dissemination—Seed production for yagrumo macho is an almost continuous process, as it is for other successional species. Seeds have a hard, impermeable outer coat; they can thus remain on the ground for a long time and still retain viability to germinate when openings in the canopy occur. When seed is collected and taken away from field conditions, the number of viable seeds is quite small and germination is extremely poor. Of over 800 individual seeds collected at one site in Puerto Rico, only 5 were viable *(21)*.

Highest germination percentages recorded were 30 percent after 70 days in Brazil and 35 percent after 40 to 90 days in Costa Rica. In Brazil the seeds were soaked for 9 to 10 hours in an unspecified chemical, covered with a thin layer of soil, and protected from direct sunlight. Seeds in Costa Rica were treated with a 3 percent solution of sodium hypochlorite *(21)*. After germination periods of 52 to 120 days, only 12 of 300 seeds germinated in three trials in Puerto Rico. Several soaking treatments with 9 *N* sulfuric acid were used. Old records from Trinidad show that treating with unknown plant hormone solutions and human urine aided seed germination.

Some 16 bird species feed on yagrumo macho seed or fruits in Puerto Rico. This may provide a plausible reason why good germination in the field cannot be duplicated in laboratory or nursery conditions. Studies have shown that after seeds are ingested by birds, they are subjected to scarification in the gizzard and chemical treatment by gastric juices in the stomach *(20)*. Although attempts to germinate seeds taken from bird feces have failed in Puerto Rico, they have been successful in Costa Rica. It is also proposed that some species feed only on the outer coat of yagrumo macho seed and others feed on the seed endosperm. Thus dormancy could be broken by mechanical puncturing or breaking of the seed coat. Until further evidence is gathered, it can be assumed that birds play the primary role in germination and dissemination of yagrumo macho seed. In Trinidad, bats also act as dispersal agents *(3)*.

Yagrumo macho seed is unwinged and heavy. Of 341 fruits and 125 individual seeds collected beneath one tree in Puerto Rico, all came from one quadrant around the tree's base.

Seedling Development—Germination is epigeous. Few studies document seedling growth of yagrumo macho in either field or nursery conditions. Early growth is fairly rapid and best when seedlings are exposed to direct sunlight. In Brazil, d.b.h. and height mean annual increments (MAI's) were 3.0 cm (1.2 in) and 1.7 m (5.6 ft) for 2-year-old plantations *(5)*. A 7-year-old plantation had mean annual height and d.b.h. increments of 1.7 m (5.6 ft) and 19 mm (0.8 in). A 20-month-old plantation in Bajo Atrato region of Colombia, planted at 3- by 3-m (9.8- by 9.8-ft) spacing, had very good form and fine branching, with a branch angle usually greater than 70°. Height and d.b.h. averaged 8 m (26 ft) and 12 cm (4.7 in) *(20)*.

Table 1—Mean annual increment by diameter classes for yagrumo macho (*Didymopanax morototoni*) measured over a 7-month period within the Luquillo Mountains in Puerto Rico (*21*)

D.b.h. classes	Mean annual increment at b.h.	Trees sampled
cm	*cm*	*no.*
	10 x 10 m quadrant	
0.0 to 0.5	0.52	2
0.5 to 1.0	0.53	9
1.0 to 1.5	0.56	6
1.5 to 2.0	0.35	3
	50 x 50 m quadrant	
0.0 to 2.5	0.86	5
2.5 to 5.0	1.30	10
5.0 to 7.5	2.46	18
7.5 to 10.0	1.40	2
in	*in*	*no.*
	33 x 33 ft quadrant	
0.0 to 0.2	0.20	2
0.2 to 0.4	0.21	9
0.4 to 0.6	0.22	6
0.6 to 0.8	0.14	3
	164 x 164 ft quadrant	
0.0 to 1.0	0.34	5
1.0 to 2.0	0.51	10
2.0 to 3.0	0.97	18
3.0 to 4.0	0.55	2

An MAI of 5.6 mm (0.22 in) in diameter was recorded in Puerto Rico for 20 individuals, where the initial overbark d.b.h. was mostly between 5 to 15 mm (0.2 to 0.6 in) (table 1). Growth was somewhat irregular when related to size class, perhaps because of crown position and the fact that some trees were exposed to direct sunlight and others were not. Mortality for the 20 individuals was 5 percent in 1 year and was attributed to vine overgrowth (*21*).

Vegetative Reproduction—Yagrumo macho wildings transplant readily and the species apparently reproduces by coppicing (*19,22*). In Puerto Rico sprouting was seen from stems broken off by wind but not on stems killed by lightning (*21*). Cuttings were used in Brazil (*5*).

Sapling and Pole Stages to Maturity

Growth and Yield—Mature yagrumo macho may reach a height of 30 m (100 ft) and a d.b.h. up to 36 cm (14 in) (*6,29*). More commonly, as in the Luquillo Mountains of Puerto Rico (*17*), the tree is of medium height and diameter, 15 to 17 m (49 to 56 ft) and 20 to 22 cm (8 to 9 in). The bole is cylindrical, swollen at the base, and has a ringed appearance. Natural pruning in the lower half is excellent (fig. 1). Yagrumo macho cannot be included in biomass estimations from regression equations because of its unusual umbrella-like crown (*8*). The outer bark is smooth and gray and the inner bark has a slightly bitter or spicy taste (*16*). Maximum age is probably between 35 and 50 years (*21*). Rooting is reportedly superficial.

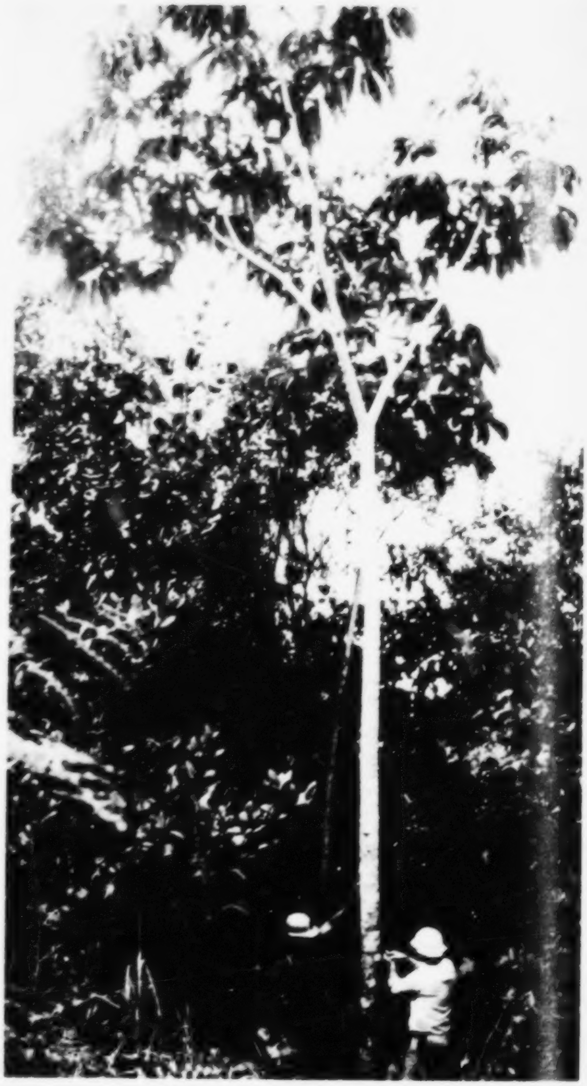

Figure 1—*Naturally regenerated yagrumo macho in the Luquillo Mountains, PR. Note the good natural pruning and umbrella-like crown.*

Table 2—Mean annual increment for yagrumo macho *(Didymopanax morototoni)* within the Luquillo Mountains of Puerto Rico, 1957 to 1975 *(9)*

Item	Sabana 8	Rio Grande	Sabana 4
Mean annual increment			
Diameter—mm	3.3	3.1	5.3
—in	0.13	0.12	0.21
Basal area—cm^2	11.1	10.6	23.4
—in^2	1.8	1.7	3.7
Trees—number	134	36	23
Elevation—m	180 to 360	420 to 600	210 to 600
—ft	590 to 1,181	1,378 to 1,968	689 to 1,968
Rainfall—mm	2290	3300	3560
—in	90	130	140

Growth or yield data for mature trees are scarce since yagrumo macho is harvested for local markets and is seldom grown under intensive plantation conditions. Limited data on diameter growth are available for older stands in Puerto Rico. Ten-year d.b.h. measurements in mature tabonuco forests in the Luquillo Mountains showed an MAI from 1.5 to 4.6 mm (0.06 to 0.18 in) *(30)*. Observed growth differences appeared to be related to crown position, with suppressed trees growing least. Eighteen-year d.b.h. measurements showed MAI rates from 3.3 to 5.3 mm (0.13 to 0.21 in) on three sites (table 2) *(9)*. The highest rate was found at Sabana 4, where yagrumo macho is a component of mature tabonuco forests. When analyzed across all three sites, growth differences between crown classes were not positively correlated with increasing crown dominance. Measurements in the Toro Negro State Forest from 1951 to 1976 showed MAI growth for yagrumo macho at 5 mm (0.2 in) *(31)*.

Mean annual d.b.h. growth rates observed in Puerto Rico do not even approach the 10 mm (0.39 in) figure sometimes quoted for mature rain forest tree species in the tropics. They are also surprisingly slow for a reportedly fast-growing successional species. Yet caution should be used in interpreting these data because of the long measurement intervals used that could cancel initial fast growth spurts occurring after successful regeneration was established (table 1).

Data from Puerto Rico for yagrumo macho and yagrumo hembra, also a successional species, show that periodic diameter growth for codominant, intermediate, and suppressed trees is comparable. This suggests that a dominant position is required before good diameter growth is shown. Finally, although periodic d.b.h. growth of older yagrumo macho in Puerto Rico was not related to initial diameter classes, it was statistically lower at lower elevations, where it was 1.9 mm (0.07 in) per year, than at higher elevations, where it was 3.7 mm (0.15 in) per year *(9)*.

Rooting Habit—No information available.

Reaction to Competition—Yagrumo macho is classed as intolerant of shade. When planted in full sunlight it exhibits its best growth and reproduction and may be very aggressive against other species. Over a 2- to 6-year d.b.h. measurement period in tabonuco forests in Puerto Rico *(1)*, MAI of yagrumo macho was 3.3 mm (0.13 in). Two more tolerant species found in the same locality, palo de matos *(Ormosia krugii)* and ausubo *(Manilkara bidentata)*, averaged 5.1 and 6.6 mm (0.20 and 0.26 in). Other work in Puerto Rico indicates that many species growing in association with yagrumo macho have larger periodic diameter increments, probably because they are more tolerant of shade *(31)*.

Few special silvicultural systems for yagrumo macho are found in existing literature. Some 30 years ago in Trinidad, a policy of "let nature heal herself" was followed when reforesting degraded or poor sites *(3)*. Yagrumo macho was one of 18 timber species whose natural regeneration was allowed to grow under a high shelterwood system *(2)*. In Brazil there are pure yagrumo macho plantations designed to produce wood for match splints *(5,27)*. Because yagrumo macho rapidly colonizes open areas and is intolerant, some sort of selective clearcutting is needed to promote adequate regeneration by natural seeding. After cutting, yagrumo macho is one of the first species to become established. It should then be one of the first to be cut for commercial use, selectively leaving more valuable species to be harvested later in the established rotation cycle.

Damaging Agents—Several agents cause damage or death to saplings or mature trees. The most common is probably wind, which can break off branches or uproot entire trees. Wind damage is most acute on very wet, steep sites where saturated unstable soils cannot provide adequate anchorage for roots. In the Luquillo Mountains, climbers or stranglers like *Clusia griesebachiana* and morning glory *(Ipomoea* spp.) are common to wetter sites and have caused branch breakage or death of larger seedlings or saplings.

Yagrumo macho is apparently free from serious diseases in nursery and field conditions, but several insects (Scarabaidae and Pyraustidae) consume either foliage or woody tree material in Puerto Rico. Young trees are sometimes killed by grazing cattle in rural areas. Clearing land for agricultural or other development often causes widespread mortality.

Special Uses

Yagrumo macho's specific gravity is between 0.35 and 0.60. Mechanical and physical properties of the wood are somewhat higher than those of yellow-poplar (*Liriodendron tulipifera*) (*6,14*). Yagrumo macho is used for general carpentry and interior construction (*18*). It is also suited for crates and boxes, utility plywood or core stock, match splints, even particleboard, and could probably be substituted for heavier grades of balsa (*16*). Felled timber is very susceptible to decay and fungal attack if not converted almost immediately. Penetration and absorption of treating solutions, either in open or pressurized tanks, is fair but can be improved considerably by incising untreated material first. Nonincised posts, cold-soaked for 5 days in a 10-percent solution of pentachlorophenol dissolved in diesel fuel, lasted from 9 to 26 years in graveyard tests in Puerto Rico. Double diffusion treatment with several chemicals gave similar results, but cold-soaking with only a 5-percent solution of pentachlorophenol dissolved in diesel fuel was far inferior, the life expectancy being only about 3 years (*7*).

Yagrumo macho leaves are used for home remedies in some countries (*16*). Special uses of the wood in Guyana include drums and canoes (*11*). Brazil has tested yagrumo macho suitability for ethanol production along with 24 other tree species (*24*). Yield was 299 liters (79 gal) per ton of raw material, close to the maximum yield of 315 liters (83 gal) per ton registered for *Protium* spp.

Genetics

Existing literature shows no references to genetic or tree breeding research for yagrumo macho. Wide natural variation in genetic traits would be expected for yagrumo macho because of its extensive natural range and the fact that it grows in several life zones under varied environmental conditions. Since there are also several other species within the same genus throughout Latin America, undescribed hybrids may exist or might be possible if species were brought together under controlled laboratory or field conditions.

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Diospyros virginiana L. Common Persimmon

Ebenaceae Ebony family

Lowell K. Halls

Common persimmon *(Diospyros virginiana)*, also called simmon, possumwood, and Florida persimmon, is a slow-growing tree of moderate size found on a wide variety of soils and sites. Best growth is in the bottom lands of the Mississippi River Valley. The wood is close grained and sometimes used for special products requiring hardness and strength. Persimmon is much better known for its fruits, however. They are enjoyed by people as well as many species of wildlife for food. The glossy leathery leaves make the persimmon tree a nice one for landscaping, but it is not easily transplanted because of the taproot.

Habitat

Native Range

Common persimmon (figs. 1, 2) is found from southern Connecticut and Long Island to southern Florida; westward through central Pennsylvania, southern Ohio, southern Indiana, and central Illinois to southeast Iowa; and south through eastern Kansas and Oklahoma to the Valley of the Colorado River in Texas. It does not grow, however, in the main range of the Appalachian Mountains, nor in much of the oak-hickory forest type on the Allegheny Plateau. Its best development is in the rich bottom lands of the Mississippi River and its tributaries and in coastal river valleys *(9)*. It is exceedingly common in the South Atlantic and Gulf States, often covering abandoned fields with a shrubby growth, and springing up by the sides of roads and fences. It is often the first tree species to start growth on abandoned and denuded cropland. It is well adapted to an environment of high insolation and low water supply.

Climate

Common persimmon grows in a humid climate throughout its range. Its best commercial development is in areas that receive an average of 1220 mm (48 in) of precipitation annually, about 460 mm (18 in) of which normally occurs during the growing season. Over the range of persimmon, the average maximum temperatures are 35° C (95° F) in the summer and -12° C (10° F) in the winter.

Soils and Topography

Common persimmon grows in a tremendous range of conditions from very dry, sterile, sandy woodlands to river bottoms to rocky hillsides and moist or very dry locations. It thrives on almost any type of soil but is most frequently found growing on soils of the orders Alfisols, Ultisols, Entisols, and Inceptisols.

Associated Forest Cover

Common persimmon is a key species in the forest cover type Sassafras–Persimmon (Society of American Foresters Type 64) *(3)* and is an associated species in the following cover types: Southern Scrub Oak (Type 72), Loblolly Pine–Shortleaf Pine (Type 80), Loblolly Pine–Hardwood (Type 82), Sweetgum–Willow Oak (Type 92), Sugarberry–American Elm–Green Ash (Type 93), Overcup Oak–Water Hickory (Type 96), Baldcypress (Type 101), and Baldcypress–Tupelo (Type 102).

Common associates are elms *(Ulmus* spp.), eastern redcedar *(Juniperus virginiana)*, hickories *(Carya* spp.), sugar maple *(Acer saccharum)*, yellow-poplar *(Liriodendron tulipifera)*, oaks *(Quercus* spp.), boxelder *(Acer negundo)*, red maple *(A. rubrum)*, sycamore *(Platanus occidentalis)*, and cedar elm *(Ulmus crassifolia)*.

Common shrub and noncommercial tree associates include swamp-privet *(Forestiera acuminata)*, roughleaf dogwood *(Cornus drummondii)*, hawthorns *(Crataegus* spp.), water-elm *(Planera aquatica)*, shining sumac *(Rhus copallina)*, and smooth sumac *(R. glabra)*.

In the alluvial bottoms of the Lower Wabash Valley, waterlocust *(Gleditsia aquatica)* and common buttonbush *(Cephalanthus occidentalis)* are close associates.

The Sassafras–Persimmon type is temporary and usually replaced with mixed hardwood types.

Life History

Reproduction and Early Growth

Flowering, Seed Production, and Dissemination—The inconspicuous flowers bloom from March to June within its botanical range and from April through May in areas where it grows best. Staminate flowers are in two- or three-flowered cymes, tubular, 8 to 13 mm (0.3 to 0.5 in) long, and greenish yellow.

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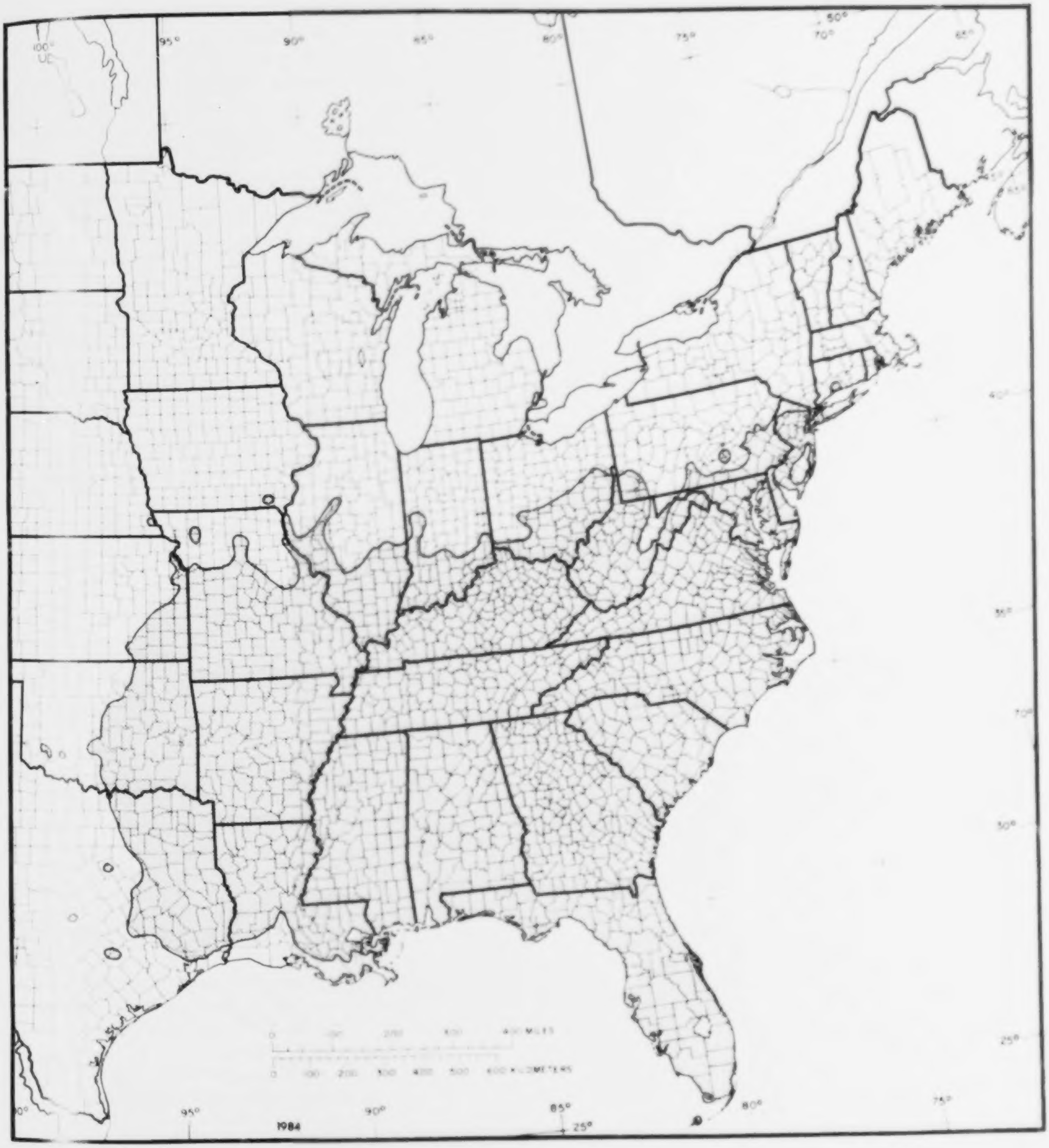
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Figure 1—*The native range of common persimmon.*

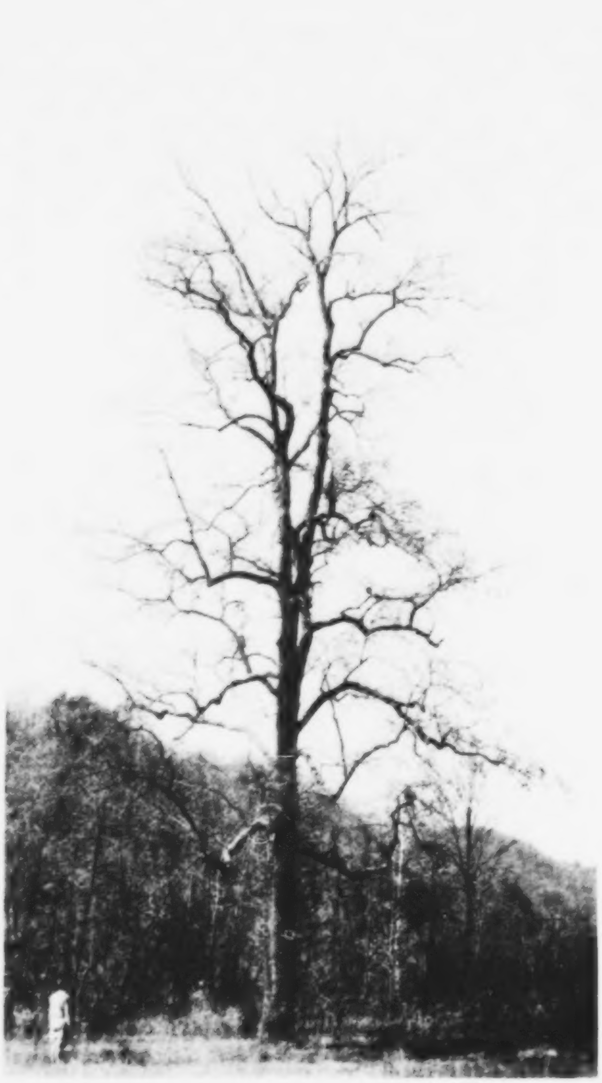

Figure 2—*Open-grown common persimmon with fruit still on the branches. The tree is 27 m (90 ft) tall and 80 cm (31 in) in d.b.h.*

Pistillate flowers are solitary, sessile or short-peduncled, about 1.9 cm (0.75 in) long. The corolla is fragrant with 4 or 5 greenish yellow, thick recurved lobes.

Common persimmon is dioecious; the staminate and pistillate flowers are borne on separate trees on shoots of the current year, when the leaves are more than half grown.

The fruit is a persistent spherical berry 1.9 to 5.1 cm (0.8 to 2.0 in) in diameter. It ripens from September to November or occasionally a little earlier. When mature it is yellow to orange or dark red in color, often with a glaucous bloom. Each berry usually contains one to eight flat, brown seeds about 13 mm (0.5 in) long but is sometimes seedless. Fruits fall from September to late winter.

The optimum fruit-bearing age is 25 to 50 years, but 10-year-old trees sometimes bear fruit. Good crops are borne about every 2 years under normal conditions. About 45 kg (100 lb) of fruit yields 4.5 to 13.6 kg (10 to 30 lb) of clean seed, with an average of 2,640 seeds per kg (1,200 seeds per lb). The seed is disseminated by birds and animals that feed on the fruits, and, to some extent, by overflow water in low bottom lands *(9)*. The seeds remain dormant during winter and germinate in April or May, after about a month of soil temperatures above 15° C (60° F).

Persimmon is easily raised from seed, and if planting is to be done with seeds, they should be cleaned and spread out for drying for a day or two and then stratified under moist conditions for 2 to 3 months at 1° to 4° C (33° to 40° F). They should be soaked 2 to 3 days before planting. Seeds lose their viability through extremes of heat, cold, or drying. They should be planted in spring or fall in shallow drills in light soils with plenty of humus and covered to a depth of about 13 mm (0.5 in).

No insects or animals are known to damage flowers or fruit seriously. Late freeze can damage the flowers and cause premature fruit drop.

Seedling Development—Persimmon is very tolerant, and natural reproduction can normally be expected in the forest understory. It is often prolific in openings. Germination is epigeal. The seedlings develop a strong taproot and after their first year are about 20 cm (8 in) tall or even taller on good sites. Prolonged flooding or submergence during the growing season will kill young trees; however, seedlings usually survive under very adverse conditions.

Vegetative Reproduction—Persimmon may be propagated by root cuttings and grafting *(10)*. Root cuttings 15 to 20 cm (6 to 8 in) long and 8 mm (0.3 in) in diameter can be used provided the ends are sealed with pitch or wax to prevent rot. Older twigs may be used similarly. They can be buried in sand until ready to plant *(15)*.

Trees may be grafted by chip budding, cleft grafting, or whip grafting. Nursery stock should be set about 15 cm (6 in) apart and root pruned each year. Stock 1 to 2 years old may be transplanted, but this should be done in moist deep soil because of the deep root system *(15)*.

Stumps sprout readily and thickets of shrubby persimmon develop from root suckers. Sprouting from the root collar after fires is common. Seedlings or suckers are difficult to transplant.

Sapling and Pole Stages to Maturity

Growth and Yield—The growth rate of persimmon is generally slow *(9)*. On dry, old-field sites it frequently makes only a shrubby growth 4.6 to 6.1 m (15 to 20 ft) tall. On poor sites the larger trees contain a high percentage of heartwood that cannot be used for lumber because it checks excessively during seasoning.

Approximately 50 percent of the total radial growth is complete in 70 to 90 days, and 90 percent complete in 100 to 109 days after growth starts in the spring *(6)*. Persimmon responds well to fertilizer.

The species normally attains a height of 9 to 18 m (30 to 60 ft) at maturity but in optimum habitats may reach a height of 21 to 24 m (70 to 80 ft) and a diameter of 51 to 61 cm (20 to 24 in). It usually forms an upright or drooping type tree with a rounded or conical crown. Stems may be clumped, either because seedlings develop in close proximity to one another or because they arise from suckers after a tree has been cut down. The leaves are deciduous, simple, alternate, and entire. The bark is brown to black, fissures are deep, and ridges are broken into rectangular checkered sections.

Per acre volume figures for this species are not available because it usually grows as scattered individuals.

Tops of orchard grown trees should be thinned to allow for better fruit production.

Rooting Habit—No information available.

Reaction to Competition—Persimmon is classed as very tolerant of shade. It can persist in the understory for many years *(9)*. Its response to release is not definitely known but is probably not especially good. Persimmon competes with almost any plant under harsh growing conditions.

Damaging Agents—A number of insects attack persimmon but normally do no serious harm *(9)*. A bark and phloem borer *(Agrilus fuscipennis)* infests living persimmon and the persimmon borer *(Sannina uroceriformis)* tunnels in the stems and taproots of young trees and damages nursery stock. Caterpillars may defoliate the trees in early summer and into mid summer. The principal defoliators are a webworm *(Seirarctica echo)* and the hickory horned devil *(Citheronia regalis)*. Unless sprayed, they may defoliate and severely damage a young plant. No serious damage to the merchantable part of living trees is recorded. The twig girdler *(Oncideres cingulata)* retards growth by cutting off smaller branches. The wood of dying and dead trees is often riddled by the false powderpost beetle *(Xylobiops basilaris)*.

Cephalosporium diospyri causes persimmon wilt, a fungus disease that kills many trees in central Tennessee and the Southeastern States *(1)*. The disease is characterized by a sudden wilting of the leaves, followed by defoliation and death of the branches from the top down. An infected tree often lives 1 or 2 years after this symptom appears. Diseased trees should be burned, and cuts and bruises on other trees should be painted to prevent entry by windborne spores. No disease-resistant trees have been found. A wound is necessary for primary infection. The hickory twig girdler and powderpost beetle cause the majority of wounds in healthy trees. As soon as the tree dies, the fungus produces spores in large quantities between the bark and the wood near the base of the tree.

Because common persimmon is often considered noxious in pastures and fields, much effort has been expended in its control and eradication *(2)*. It is easily defoliated with 2,4,5-T at 1.1 kg/ha (1 lb/acre) or less but sprouts readily from both stem and roots after treatment. Treatment is most effective in May when leaves are fully expanded. Additives (Ethephon, MAA, and TIBA) increase both the defoliation and kill of persimmon. Surfactants increase effectiveness of 2,4,5-T. Picloram in combination with 2,4,5-T, and dicamba, alone and in combination with 2,4,5-T, has also given good control. Soil application of picloram and dicamba at 6.7 kg/ha (6 lb/acre) gave kills of 75 and 70 percent, respectively. Complete top kill was possible by injecting undiluted solutions of dicamba or mixtures of 2,4,5-T and dicamba.

Tordon 101 or Esteron 99 at 7.6 liters (2 gal) plus triclopyr at 9.4 liters/ha (1 gal/acre) and Tordon at 37 liters/ha (4 gal/acre) gave 100 percent control of persimmon *(4)*.

Undiluted 2,4-D dimethylamine killed persimmon when applied in 1- or 2-ml (0.03- or 0.07-oz) dosages in injections placed edge-to-edge up to 23 cm (9 in) apart around the stem *(11)*. A 4-to-1 mixture of triisoproponolamine salts of 2,4-D plus picloram was also effective.

Special Uses

The wood is heavy, hard, strong, and very close grained. The average number of rings is 5.5 per cm (14 per in) *(12)*. Specific gravity of light-brown sapwood is 0.79; a 0.028 m^3 (1.0 ft^3) block weighs about

22 kg (49 lb). Because of its hardness, smoothness, and even texture, it is particularly desirable for turnery, plane stocks, shoe lasts, shuttles, and golf club heads.

Persimmon is sometimes planted for its edible fruit. Dried fruit is added to baked goods and occasionally is fermented with hops, cornmeal, or wheat bran into a sort of beer. The dried, roasted, ground seeds have been used as a substitute for coffee.

Several cultivars are available with improved fruit size and quality. In native persimmon areas, top working or grafting on suckers is a good way to get superior cultivars into bearing quickly. One staminate tree seems sufficient to pollinate at least 23 pistillate trees of the same race *(8)*. The pulp is very astringent when not ripe, but after a frost in the fall, when the fruit turns yellow orange, the flesh is pleasing in taste *(12)*. The fruit is eaten by many species of song birds, also by the skunk, raccoon, opossum, gray and fox squirrels, white-tailed deer, wild turkeys, bobwhite, crows, rabbits, hogs, and cattle *(5)*. It may, however, cause sickness in livestock. Deer browse readily on persimmon sprouts, but cattle graze them only lightly.

Seeds and fruits are generally low in crude protein, crude fat, and calcium but high in nitrogen-free extract and tannin *(13)*.

The inner bark and unripe fruit are sometimes used in treatment of fevers, diarrhea, and hemorrhage. Indelible ink is made from fruit.

Persimmon is valued as an ornamental because of its hardiness, adaptability to a wide range of soils and climates, its lustrous leaves, its abundant crop of fruits, and its immunity from disease and insects. It has been introduced into Europe.

The tree is suitable for erosion control on deeper soils because of its deep root system, but this same characteristic makes it difficult to plant.

Persimmon is considered a woody weed in unimproved pastures, and it prevents many areas from being grazed effectively. Inoculation of persimmon stumps with a fungus *(Cephalosporium diospyri)* was found to be an effective means of preventing subsequent sprouting.

Persimmon flowers are useful in the production of honey.

Genetics

Varieties of the common persimmon are the fuzzy common persimmon *(D. virginiana* var. *pubescens* (Pursh) Dipp.); Oklahoma common persimmon *(D. virginiana* var. *platycarpa* Sarg.); and Florida persimmon *(D. virginiana* var. *mosieri* (Small) Sarg.) *(7)*.

Hybrids have been reported between *D. virginiana*, *D. kaki*, and *D. lotus (14)*.

Several cultivars, selected primarily for fruit color, taste, size, and early maturation, have been chosen from wild populations *(8)*.

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Eucalyptus globulus Labill. Bluegum Eucalyptus

Myrtaceae Myrtle family

Roger G. Skolmen and F. Thomas Ledig

Bluegum eucalyptus *(Eucalyptus globulus)*, also called Tasmanian bluegum, is one of the world's best known eucalyptus trees. It is the "type" species for the genus in California, Spain, Portugal, Chile, and many other locations. One of the first tree species introduced to other countries from Australia, it is now the most extensively planted eucalyptus in the world.

Habitat

Native Range

Four subspecies are recognized. The type tree, subspecies *globulus*, is largely confined to the southeast coast of Tasmania but also grows in small pockets on the west coast of Tasmania, on islands in the Bass Strait north of Tasmania, and on Cape Otway and Wilson's Promontory in southern Victoria, Australia *(9)*. Other subspecies are found northward in Victoria and New South Wales *(13)*.

The species was introduced into California in 1856 *(1)* and into Hawaii about 1865 *(18)* and has become naturalized in both States. It is also fairly common as an ornamental in Arizona but is not naturalized there. In California, it is now primarily used in line plantings along roads and as windbreaks, but formerly, extensive plantations were established. Plantings total about 16 000 ha (40,000 acres) *(17)*. The planted range in California extends from Humboldt County in the north to San Diego County in the south, with best growth in the coastal fog belt in the vicinity of San Francisco. Numerous plantings are seen in the Central Valley from Redding, south through Fresno to Bakersfield, and San Bernardino. Hawaii has about 5000 ha (12,000 acres)—almost all of them on the islands of Hawaii and Maui. In California and Hawaii the tree regenerates within and near the edges of plantations. In some areas of Hawaii it spreads fast enough to be considered a pest by ranchers.

Recently, the species has also been planted in its native Tasmania where it is an important pulpwood source *(22)*.

Climate

Although bluegum eucalyptus has great climatic adaptability, the most successful introductions worldwide have been to locations with mild, temperate climates, or to high, cool elevations in tropical areas *(8)*. The ideal climate is said to be that of the eastern coast of Portugal, with no severe dry season, mean annual rainfall 900 mm (35 in), and minimum temperature never below −7° C (20° F). In coastal California, the tree does well in only 530 mm (21 in) rainfall accompanied by a pronounced dry season, primarily because frequent fogs compensate for lack of rain. A similar situation is found in Chile where deep fertile soils as well as fogs mitigate the effect of low, seasonal precipitation *(8)*. In Hawaii, bluegum eucalyptus does best in plantations at about 1200 mm (4,000 ft) where the rainfall is 1270 mm (50 in) annually and is evenly distributed or has a winter maximum. Seasonality of rainfall is not of critical importance to the species. Although it generally grows well in countries with a Mediterranean or cold season maximum rainfall, it grows well also in summer rainfall climates of Ethiopia and Argentina *(8)*.

Soils and Topography

Bluegum eucalyptus grows well on a wide range of soils. It requires good drainage, low salinity, and a soil depth of about 0.6 m (2 ft) or more. Other limiting factors are few *(8)*. In locations with a pronounced dry season, such as California, the tree grows best on deep alluvial soils because of the greater moisture supply.

In Hawaii, the tree grows very well on Typic and Hydric Dystrandepts, soils of the latosolic brown forest great soil group. These soils are generally 0.9 m (3 ft) deep, acid in reaction, and formed on volcanic ash. In California, the tree grows well on a much wider range of soils than in Hawaii, from the Ultisols and Alfisols developed on deeply weathered sedimentary deposits and sandstone to Inceptisols and Aridisols developed on a wide variety of parent materials.

In Portugal, almost 15 percent of the land area is planted to this species. Most stands are on soils developed from sandstone and limestone, which have been badly degraded by cultivation since ancient times. Best yields occur on the heavy texture clay-loams and clays *(11)*.

Associated Forest Cover

In its native habitat, bluegum eucalyptus grows in pure stands and in mixture with messmate stringy-

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bark eucalyptus (*Eucalyptus obliqua*), mountain-ash eucalyptus (*E. regnans*), manna eucalyptus (*E. viminalis*), black peppermint eucalyptus (*E. amygdalina*), and white peppermint eucalyptus (*E. pulchella*). Although, for the most part, it has been planted in pure plantations in countries where it has been introduced, it has also been planted in mixture. In California, it has most commonly been mixed with forest redgum eucalyptus (*E. tereticornis*) and river redgum eucalyptus (*E. camaldulensis*) *(19)*. In Hawaii, it has been planted in mixture with many other eucalypts.

Most of the dense bluegum eucalyptus stands in California and Hawaii are noted for being almost devoid of understory vegetation, except for a few hardy grasses. Although this condition is most likely related to the rather dry climate that provides the best site for the species, it has also been shown that the leaves of the tree produce water soluble phytotoxins that can prevent radicle growth of many herbaceous plants *(7)*. In Hawaii, firetree (*Myrica faya*) is a species that sometimes invades bluegum eucalyptus stands. The noxious passion fruit vine (*Passiflora mollissima*) has also been found thriving in a young coppice stand.

Life History

Reproduction and Early Growth

Bluegum eucalyptus has a considerable competitive advantage as compared with most other tree species in that its juvenile foliage is seldom browsed by cattle or sheep (fig. 1) *(8)*. This condition not only caused it to be a popular tree for planting in open grasslands years ago, but it permits natural seedlings to survive in the presence of grazing animals alongside the planted stands. The tree reproduces by seeding into openings in planted stands and into fields adjacent to plantations.

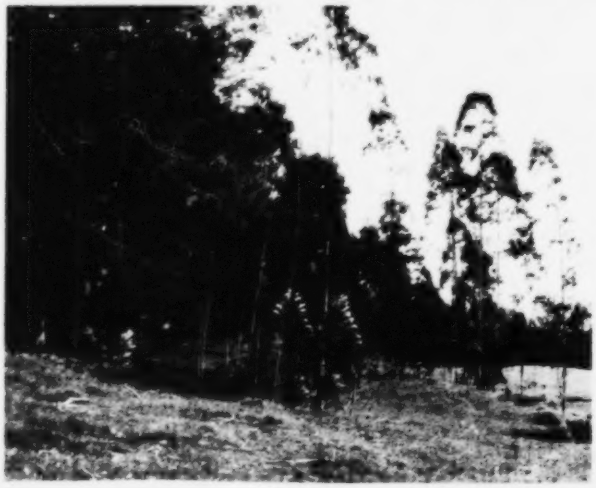

Figure 1—*Bluegum eucalyptus, showing how it readily seeds into grasslands adjacent to planted stands. It spreads rapidly (if not controlled) because cattle do not graze the seedlings.*

Seed stored in the soil under older stands often germinates prolifically following logging and the resultant natural reproduction interferes with the management of the coppice stand *(21)*.

Flowering and Fruiting—Bluegum eucalyptus in California flowers from November to April, the wet season *(15)*. In Hawaii, some trees flower throughout the year, but flowering is heaviest in February to March. The flower buds have a warty cap or operculum about 2.5 cm (1 in) in diameter, which falls off, allowing the very numerous stamen filaments to extend in shaving-brush fashion above the cup-shaped base (hypanthium). The yellowish white flowers are pollinated by insects, hummingbirds, and other pollen and nectar feeders. As in almost all eucalyptus, pollen is usually viable before the stigma becomes receptive *(8)*. The fruit, a distinctive top-shaped woody capsule 15 mm (0.6 in) long and 2 cm (1 in) in diameter, ripens in October to March in California, about 11 months after flowering *(15)*. In Hawaii the fruit ripens throughout the year.

Seed Production and Dissemination—Bluegum eucalyptus seeds are relatively large for a eucalyptus. There are 18 to 320 seeds per gram (500 to 9,100/oz) of seeds and chaff, or about 460 clean seeds per gram (13,000/oz) *(2,5,15)*. Capsules release seed immediately on ripening and the seed is dispersed by wind. Calculated dispersal distance from a 40-m (131-ft) height, with winds of 10 km/hr (6 mi/hr), was only 20 m (66 ft). Newly released seeds germinate within a few weeks if conditions are suitable. Trees usually begin to produce seeds at 4 to 5 years and yield heavy seed crops in most locations at 3- to 5-year intervals *(23)*. Seeds can be stored for long periods in air-tight containers at 0° to 3° C (32° to 38° F).

Seedling Development—Newly germinated seedlings have inverse heart-shaped cotyledons, borne epigeously. The stems of seedlings, especially those grown in the shade, are usually square in cross section, often for as much as 3 to 5 m (10 to 16 ft) of stem length. These square stems usually have prominent ridges or "wings" at the corners. Juvenile leaves, which are opposite and broadly lanceolate, 9 by 9 cm (3.5 by 3.5 in), may persist for more than a year *(9)*. Trees in coppice stands 6 m (20 ft) or more in height are often entirely in the juvenile leaf form. These juvenile leaves bear a bluish gray, waxy bloom and are the reason for the common name of the tree, bluegum.

Nursery-grown seedlings in containers reach plantable size, about 30 to 40 cm (12 to 16 in) high, in 3 to 4 months. Seedlings can be established if planted with bare roots, but success is highly dependent on favorable wet weather after planting. Seedlings are, therefore, usually grown in containers and planted with a root ball. Seedlings are not frost resistant *(23)*.

With favorable weather conditions on good sites in Hawaii, seedlings that germinate after logging and are not suppressed can be expected to be 1 m (3 ft) tall at 6 months, 2 m (6 ft) at 1 year, and 4 m (13 ft) at 2 years. Seedlings in four coppice stands in Hawaii grew poorly because they were generally suppressed by coppice shoots from stumps *(21)*. Despite this, an average annual growth of 1.1 cm (0.4 in) in diameter at stump height and 1.4 m (4.6 ft) in height was recorded for all seedlings in stands 3, 4, 5, and 6 years old. Stocking of seedlings and coppice shoots in these stands was high, averaging more than 6,000 stems per hectare (2,400/acre). Measurements in six representative planted stands in California that were 5 years or less in age gave an average annual height growth of 2 m (6.7 ft) *(19)*. In Victoria, Australia, unfertilized planted seedlings grew 1 m (3 ft) annually during a 4-year period, while fertilization of seedlings at three different levels nearly doubled the growth rate *(6)*. Bluegum eucalyptus seedlings show a strong response to nitrogen and phosphorus fertilization on many soils *(23)*.

Vegetative Reproduction—Bluegum eucalyptus coppices readily from stumps of all sizes and ages. Stumps should be cut 10 to 20 cm (4 to 8 in) high in stands managed for coppice *(23)*. Low-cut stumps do not coppice well from the lignotuber, and coppice stems from stumps cut higher tend to break off easily in the wind. Because the buds that sprout are on the bark side of the cambium and initially weakly connected to the wood of the stump, it is essential that the bark be firmly attached to the stump if coppice stems are to survive. In four coppice stands in Hawaii, ranging in age from 2 to 6 years after logging, annual growth of stump coppice averaged 15 mm (0.6 in) in diameter at stump height and 1.8 m (5.9 ft) in height *(21)*. This growth was considerably better than that of seedlings in the same stands referred to earlier.

Elsewhere than Hawaii, where foresters have had no experience beyond one rotation, bluegum eucalyptus is normally carried for three coppice rotations after the first, or seedling rotation. Rotations range from 5 to 10 years in different countries and sites. Undesirable shoots are usually removed during the first 2 years of a coppice crop, but thinning is normally not done. In Portugal, coppice stands are sometimes managed by the system of "coppice with standards" so that a sawtimber crop of the straightest and best trees is retained between coppice harvests to be cut as sawtimber when of suitable size *(8)*.

In Portugal, coppice rotations are 10 to 15 years with annual yields normally 15 to 20 m^3/ha (214 to 286 ft^3/acre) *(11)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Bluegum eucalyptus is considered a fast-growing tree in most countries where it is used, but a wide range of growth and yield figures are reported in the literature. We know of no data for natural stands in Australia, but some plantations in Tasmania, Victoria, and the Australian Capital Territory (A.C.T.) have done well *(3)*. In Tasmania, a yield of subspecies *globulus* at 17 years of 35 m^3/ha (500 ft^3/acre) per year was reported, with the tallest trees averaging 30 m (99 ft). A plantation of ssp. *globulus* in Victoria averaged about 20 cm (8 in) in d.b.h. and 18 m (59 ft) in height at 14 years, while another (ssp. *bicostata*) at Canberra, A.C.T., at age 13 and somewhat lower stocking, averaged 21 cm (8.3 in) in d.b.h. and 15.5 m (51 ft) in height *(3)*.

These data are well within the range of those reported for other countries *(8)*. Annual growth in northwestern Spain averages 20 m^3/ha (286 ft^3/acre), but in southwestern Spain only 5 to 6 m^3/ha (71 to 86 ft^3/acre). In Uruguay, 25 m^3/ha (375 ft^3/acre) of annual growth is considered good. In Ethiopia and Portugal, at age 10 on the highest quality site, very good growth is 20 m^3/ha (286 ft^3/acre) per year.

In California, 67 different stands were measured in 1924 *(19)*. The mean annual growth of all these stands ranging from 2 to 42 years in age, was 19 m^3/ha (271 ft^3/acre). Ten of these stands, ranging from 13 to 16 years in age and similar to the plantation in Australia, averaged 19.6 cm (7.7 in) in d.b.h., and 20.4 m (67 ft) in height, and had a mean annual growth of 21 m^3/ha (300 ft^3/acre). The tallest stand averaged 38.7 m (127 ft) at 23 years. The tallest stand in California is one planted in 1877 on the University of California campus at Berkeley; it contains trees that have been more than 61 m (200 ft) tall since 1956 (fig. 2) *(1)*.

In Hawaii, 20 stands ranging in age from 2.5 to 35 years were evaluated in 1911 *(18)*. Four of the stands were in the age range 11 to 20, somewhat similar to the plantations in Australia. In these four, the average d.b.h. was 29.2 cm (11.5 in), and average height was 23 m (76 ft). The tallest stand averaged 30.5 m (100 ft) at 14 years. Seven stands ranging in age from 5 to 20 years had an average annual yield of 20 m^3/ha (286 ft^3/acre). The tallest bluegum eucalyptus trees in Hawaii were at Kukaiau Ranch, on the Island of Hawaii, and were about 61 m (200 ft) tall until logged at age 70.

Rooting Habit—Bluegum eucalyptus generally does not form a taproot. It produces roots throughout the soil profile, rooting several feet deep on soils that permit it, or shallowly otherwise. On shallow soils, subsoiling to permit greater depth of rooting has markedly improved growth *(8)*. On most trees all the roots are below the lignotuber, but occasionally, adventitious roots result from layering of the stem above the lignotuber. The tree is windfirm by the time it reaches sapling size, but because the root system develops slowly, it can be windthrown when a seedling.

Reaction to Competition—Bluegum eucalyptus is generally classed as intolerant of shade and planted stands quickly develop crown differentiation as soon as the crowns close. On sites for which it is best suited, other species cannot compete with it. In Australia, it frequently grows in mixed stands because of microsite variation that favors the competing species that have evolved in the area *(23)*.

Although leaves of the species produce water-soluble toxins that may help prevent competition by larger trees *(7)*, one or two maintenance cleanings are usually required shortly after planting to free seedlings from being overtopped by grasses. In Hawaii, sprouts from buried lignotubers often grow as much as 30 cm (12 in) horizontally through litter and grass before emerging to light.

Damaging Agents—Although bluegum eucalyptus is seldom browsed by cattle or sheep, seedlings are often severely girdled by rodents. This condition can be prevented by cultivating around the young trees to remove the protective cover the rodents require *(19)*. Although grazing animals do not eat the trees, they do trample them and should be excluded from young plantations.

In California, bluegum eucalyptus stands are highly susceptible to fire during the dry season. The bark, which hangs in strips from the stems, readily carries fire into the crowns, and the leaves contain volatile oils that produce a hot fire. Trees are rarely killed by fire, however, as they sprout vigorously from the stems and bases *(8)*. In the moister climate of Hawaii, fire has not been a problem in bluegum eucalyptus stands.

Seedlings are intolerant of frost and temperatures of -5° to -10° C (23° to 14° F) usually kill them. Frost resistance increases with maturity, juvenile foliage being less resistant than mature foliage *(4)*. In 1972 a severe frost in the hills of Berkeley, CA, completely defoliated most of the mature bluegum eucalyptus. The trees were considered dead by several authorities and a salvage logging program was started to remove the fire hazard. A few months later, most of the "dead" trees sprouted from the stems and bases and began to grow again. This sprouting was judged undesirable and several experiments were undertaken aimed at preventing it. The most successful treatment found was to flood axe frills made at the tree bases with a 0.36 kg/1 (3 lb/gal) solution of glyphosphate in water *(10)*. This permanently killed the trees.

The tree is susceptible to drought, particularly on shallow soils. On such soils, subsoiling has been used effectively to permit deeper rooting and to overcome drought susceptibility.

Several insects attack bluegum eucalyptus, although none has been a serious problem in California

Figure 2—*Bluegum eucalyptus stand, planted in 1877 on the campus of the University of California, Berkeley.*

or Hawaii. One that is common in many parts of the world is the wood borer, *Phoracantha semipunctata*, which has caused severe damage in South Africa and Western Australia. A scale insect, *Eriococcus coriaceus*, has caused high mortality in New Zealand. Several defoliating insects in the genera *Gonipterus*, *Chrysophtharta*, and *Mnesampela*, attack the species.

Fungi have generally not been a severe problem with bluegum eucalyptus. Damping off in nurseries caused by *Botrytis cinerea* has been a problem but is easily controlled. *Pythium* and *Rhizoctonia* spp. have also caused damping-off in containers and flats, particularly when old seed was used *(16)*. *Fusarium* spp. have destroyed quantities of stored seed in Spain. Attack by *Diplodia* and *Armillaria* has been reported from several countries, but neither disease is considered serious *(8,23)*.

Special Uses

Bluegum eucalyptus is one of the world's most valuable windbreak trees because of its windfirmness and the unpalatable nature of its seedlings to grazing animals *(8,18,19)*. Because of its ability to sprout along the stem, it can be hedged, thereby making effective sight and sound barriers along highways. The horticultural variety *compacta* is a dwarf form widely used along California freeways. Bluegum eucalyptus windbreaks are most effective with an understory or adjacent planting of smaller trees and shrubs *(20)*.

The species is a major source of fuelwood in many countries of the world primarily because of its ability to coppice after cutting. The wood burns freely, leaves little ash, and produces good charcoal *(8)*. The tree shows promise for use as industrial fuelwood in place of oil. Closely spaced and fertilized plantings in Victoria, Australia, produced mean annual increments of 9 to 14 metric tons per hectare (4 to 6 tons/acre) dry weight of stem wood during a 4-year period *(3)*. In Hawaii, untended 3- to 6-year-old coppice stands average stem wood dry weights of 5 to 7 t/ha (2 to 3 tons/acre) per year. One stand, during its fifth year of growth, produced 14 t/ha (6 tons/acre). Another, during its second year, produced 8 t/ha (3.6 ton/acre) *(20)*.

Bluegum eucalyptus is much used for pulpwood, particularly so because its bark, acceptable in most pulping processes, adds greatly to the yield. It is used mostly for bleached products made by sulfate, sulfite, or bisulfite processes *(8)*.

Other uses include the extraction of essential oils from the leaves, honey production from the flowers (that are also good pollen sources), plantings for erosion control, and roadside plantings to provide a noise and headlight buffer *(8)*.

Because the wood is heavy and shrinks greatly in drying, it is unsuitable for lumber. Sawing of logs is difficult and the quality of lumber is poor because of growth stress problems. Main uses of bluegum eucalyptus are for mining timber, fence posts, and poles *(23)*. In South America, the straight, uniform poles are used extensively in construction *(17)*. Lumber and veneer are produced on a fairly large scale in Portugal and Spain where the wood is used for cooperage, furniture, and flooring *(8)*. A small amount of lumber used to be produced in Hawaii.

Genetics

Population Differences

Several previously described species, southern bluegum (*E. bicostata* Maiden *et al.*), Maiden's gum (*E. maidenii* F. Muell.), and *E. pseudoglobulus* Naudin ex Maiden, have been reduced to subspecies of bluegum eucalyptus (*E. globulus* ssp. *globulus*) *(12)*. Steep clines are found in many fruit and vegetative characteristics across the subspecies boundaries, and more gradual changes appear within the ranges of the four subspecies in Australia. The ssp. *pseudoglobulus* is central, grading on different borders into each of the other three subspecies. The most frost-hardy seedlings originate from populations above 450 m (1,475 ft) elevation in the ranges of ssp. *bicostata* and ssp. *maidenii*, but these tend to be the oldest growing *(13)*. Tasmanian bluegum eucalyptus, ssp. *globulus*, originating near sea level in the southern part of the species range, is the most rapidly growing. Within taxa, drought tolerance of seedlings is associated with populations native to the driest sites. Variation in glaucous bloom of the leaves is correlated with elevation and the "bluer" forms are more frost hardy and more drought tolerant than the "greener" forms. Variations are known, such as California bluegum eucalyptus var. compacta (Hort.), a cultivar propagated in the nursery trade for its compact habit and widely used along California highways (2,20).

Hybrids

Natural or controlled hybrids of bluegum eucalyptus with *E. blakelyi*, *E. botryoides*, *E. cinerea*, *E. cypellocarpa*, *E. ovata*, *E. rudis*, *E. tereticornis*, *E. urnigera*, and *E. viminalis* are known *(8,14,18)*.

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Eucalyptus grandis Hill ex Maiden **Rose Gum Eucalyptus**

Myrtaceae **Myrtle family**

George Meskimen and John K. Francis

Eucalyptus grandis is native to the east coast of Australia. Its common name is rose gum or flooded gum (a misnomer). Rose gum is one of the premier forest species in the Australian States of Queensland and New South Wales where it grows 43 to 55 m tall (140 to 180 ft) and 122 to 183 cm (48 to 72 in) in diameter *(15)*. Its form is excellent with tall, straight, clean boles up to two-thirds of the total height. The bark is thin and deciduous, shedding in strips to expose a smooth surface marked with flowing patterns of silvery white, slaty gray, terra cotta, or light green. Occasionally a "stocking" of light-gray, platelike or fissured bark persists over the basal 1 to 2 m (3 to 6 ft) on the trunk.

Rose gum is one of the most important commercial eucalypts, with more than one-half million hectares (1.3 million acres) planted in tropical and subtropical areas on four continents. Massive planting programs have been carried out in the Republic of South Africa and Brazil, and there are substantial plantings in Angola, Argentina, India, Uruguay, Zaire, Zambia, and Zimbabwe *(21)*. In southwest Florida rose gum may be an emerging commercial species for plantations. It has been successfully tested for pulpwood and fuel; and its wood has potential for poles, pallets, veneer, and other products. In California, Hawaii, and Puerto Rico, rose gum appears in some species trials and landscaping.

Habitat

Native Range

Over its central range, rose gum grows on alluvial or volcanic loams in valleys and flats within 160 km (100 mi) of the coast, straddling the Queensland–New South Wales border from latitude 26 to 33° S. Two outlier populations extend the range to the Atherton Tablelands at latitude 13° S. *(10,15)*.

In Florida, intensive research on rose gum began in 1961 and operational planting in 1972. Through the 1980 planting season, it was commercially planted on 5,650 ha (14,000 acres) in Glades, Hendry, and Charlotte Counties in southwest Florida between latitude 26° 31′ and 27° 02′ N. and between longitude 81° 31′ and 81° 48′ W. Outside that zone there are numerous potential planting areas in south Florida.

Climate

The climate in the Australian native range of rose gum is humid subtropical with mean minimum temperatures during the coldest month ranging from 2 to 10° C (36 to 50° F) and mean maximums near 29° C (85° F) during the hottest month. Rainfall averages 1020 to 1780 mm (40 to 70 in); it is concentrated in the summer, but monthly precipitation during the dry season is at least 20 mm (0.8 in) *(10,21)*. Coastal areas are generally frost-free, but higher altitude, inland areas experience occasional frosts *(6)*.

Southwest Florida is humid and subtropical. Summers are long, rainy, and warm; winters are dry and mild but with the threat of damaging frost. Mean annual rainfall ranges from 1270 to 1400 mm (50 to 55 in). Monthly precipitation during the rainy season, June through September, averages about 180 to 200 mm (7 to 8 in). Rainfall during the dry season, November through April or May, averages 50 mm (2 in) per month *(40)*. Dry-season rainfall is unreliable, however. Daily maximum temperatures from late May through September exceed 32° C (90° F) on most days but rarely reach 38° C (100° F). During the coldest month, daily maximum temperatures average near 24° C (75° F) and daily minimums near 11° C (52° F) *(27)*. But swift continental cold fronts change balmy afternoons into dangerously cold nights. The lowest temperatures recorded in each of 30 winters averaged –4.4° C (24° F) *(22)*.

Soils and Topography

This species grows on flats or lower slopes of deep, fertile valleys in Queensland and New South Wales. It grows best on moist, well drained, deep, loamy soils of alluvial or volcanic origin *(6)*. Clayey soils are acceptable if they are well drained *(23)*.

The rose gum plantations in Florida lie in a physiographic region known as the Western Flatlands *(11)*. Topography is nearly flat; elevations change almost imperceptibly from coastal sea level to 6, 12, or rarely 18 m (20 to 60 ft) elevation inland. Soils are almost exclusively members of the sandy, siliceous hyperthermic Haplaquods. Derived from

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marine deposits, these soils are mainly sands, strongly acid, poorly drained, and underlain by spodic horizons that are commonly impervious to root penetration and water drainage. The combination of high seasonal rainfall, flat topography, and low elevation results in high water tables, shallow root zones, and local inundation during the rainy season. Conversely, during the dry season these sandy soils rapidly become moisture deficient.

Associated Forest Cover

In its native range, rose gum grows in tall, open forests associated with the eucalypts *E. intermedia*, *E. pilularis*, *E. microcorys*, *E. resinifera*, and *E. saligna*, as well as *Syncarpia glomulifera*, *Tristania conferta*, and *Casuarina torulosa*. Rose gum also commonly grows on the fringes of and occasionally within rainforest *(6)*. In Florida, rose gum plantations are most frequently established on palmetto prairies. The characteristic vegetation of palmetto prairies consists of a ground cover of *Serenoa repens*, *Aristida stricta*, *Andropogon* spp., *Myrica pusilla*, *M. cerifera*, *Ilex glabra*, and *Quercus minima*, with the scattered trees, *Sabal palmetto*, *Quercus virginiana*, and *Pinus palustris (12)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Rose gum, like all eucalypts, bears perfect flowers. Buds form in axillary umbels with usually seven buds per cluster. Each flower consists of a central style surrounded by stamens standing about 8 mm (0.3 in) tall and forming a bloom about 20 mm (0.8 in) in diameter. The puffy clusters of creamy white blooms are attractive and conspicuous but not of horticultural quality.

The main blooming season is mid-August through late September, but some trees start blooming early in August and the latest finish in mid-November. This blooming season of late summer-early fall matches the low-elevation blooming season in South Africa but contrasts with the late fall-early winter bloom at high elevations *(18)* and the midwinter bloom in Australia *(5)*. Each tree blooms serially over a period of 5 to 10 weeks, with an average of only 12 percent of a tree's bud crop in prime bloom during a given week.

Foraging insects, particularly honeybees, pollinate the flowers. In an individual flower, the stigma is not receptive until after pollen shed, but because each tree blooms serially, there is, unfortunately, ample opportunity for self-fertilization. In a South African seed orchard, selfing occurred with a frequency of 10 to 38 percent, caused 10 recognizable detrimental abnormalities, and depressed the height growth of outplanted seedlings 8 to 49 percent compared to crossed progenies *(19)*. Flowering precocity is strongly inherited; a few families bloom at plantation-age 1 year, many more at age 2, and 97 percent of the orchard at age 3.

From 2 to 3 weeks after blooming, the stamens and style wither and fall away, leaving a woody, urn-shaped seed capsule closed by four to six valve covers. The capsules are about 8 mm long by 6 mm in diameter (0.3 by 0.25 in). Most umbels carry five to seven capsules to maturity.

Seed Production and Dissemination—Seed capsules are mature for harvest 6 or 7 months after flowering. However, the capsules remain closed on the tree for at least 1 year after maturity, so it is possible to gather two seed crops at a time by harvesting in alternate years. Seed capsules should be harvested by severing the umbel stalks; the alternative of clipping seed-bearing twigs reduces the next flower crop.

The valves of the capsules dry out, open, and release seeds. Capsules scattered loosely on a dry surface release their seeds after about 2 hours in full sun. Commercial bulk lots can be extracted in about 1 week in chambers equipped with open-mesh shelves, heating from 30 to 35° C (86 to 95° F), forced-air circulation, and dehumidification.

Individual trees bear from 3 to 25 sound seeds per capsule, with an average near 8 *(20)* and a much greater mass of infertile ovules called "chaff." Fertile seeds are tiny, only about 1 mm (0.04 in) in diameter. Chaff particles are lighter colored and only minutely smaller and lighter than seeds. Seed cleaning involves sorting by size and shape through multiple sieves, then separating by weight in a pneumatic separator.

In Florida, operational quantities of seeds can be harvested from an orchard at age 3.7 years and production increases annually to a plateau at about age 10. Seed production is reliable year to year, but there is great tree-to-tree variation in the quantity, purity, and viability of seed crops. The 1-year seed crop from some 7-year-old trees was as follows:

Volume of uncleaned seeds, liters	1.70
quarts	1.80
Weight of uncleaned seeds, kg	0.99
lb	2.18
Healthy germinants per gram	688
per ounce	19,504
Healthy germinants per tree	694,115

Seeds have been successfully stored for 20 years by either freezing at –8° C (18° F) or refrigerating at

10° C (50° F). Rose gum seeds require no presowing treatment.

Seedling Development—Germination of rose gum is epigeal and takes place in 7 to 1[illegible] days after sowing *(4)*. Moist, bare soil is required for natural regeneration; fire, erosion, and flood deposits provide satisfactory seedbeds. In commercial forests, the species is almost always regenerated by planting. Seedlings are usually raised to 20 to 30 cm (7.8 to 11.8 in) tall, which takes 3 to 5 months *(29)*. Due to the sensitivity to desiccation, seedlings are normally grown in containers. Rigid containers with multiple cavities from which the seedlings are removed with roots and soil intact are almost always used in large operations. Seedlings are also grown in plastic nursery bags. In the absence of frost and drought, seedlings can be planted throughout the year. In many areas seedling production and planting must be carefully timed. In Florida, planting must coincide with summer rains to give sufficient time for seedlings to grow into hardy saplings before facing winter frosts.

Site Preparation and Planting in Florida—Success in establishing rose gum in plantations depends on double chopping or cross disking to greatly reduce vegetative competition, then broadcasting 1.12 t/ha (0.5 ton/acre) of ground rock phosphate to overcome a severe natural phosphorus deficiency, and finally bedding to elevate the seedlings out of the standing water during the first rainy season *(25)*. Saw-palmetto rhizomes are thick, fibrous, and deeply rooted, requiring heavy equipment for chopping and bedding. Landowners prepare sites in the spring when the deepening drought enhances the kill from chopping or disking. Also, spring offers little time or moisture for weed competition to colonize the beds before summer planting starts.

Planting crews use high-clearance wheel tractors to straddle the beds and pull planting machines fitted with racks holding four cartons containing a total of 1,400 to 2,000 containerized seedlings. This number is sufficient to traverse several rows as long as 1 km (0.6 mi). Recommended planting density is 1,495 seedlings per hectare (605 seedlings/acre) on beds spaced 3.7 m (12 ft) apart and seedlings spaced 1.8 m ([illegible] ft) along the beds *(26)*.

In the first 2 years of machine planting, survival averaged 86 percent in an extremely wet season and 75 percent in a dry year. Survival after machine planting probably averages about 84 percent. Hand planting routinely achieves at least 95 percent survival.

Vegetative Reproduction—After harvest, under favorable conditions, rose gum plantations regenerate by coppicing (sprouting) from the stumps. Two or three coppice rotations are commonly harvested before it is necessary to replant seedlings. Coppice shoots initially grow faster than seedlings, but that advantage is partially offset by stump mortality, which usually runs about 5 percent per rotation in South Africa *(39)*. In many areas, coppice forms equally well regardless of the season of harvest. In Florida, however, it was shown that summer harvests (June-September) reduced coppicing ability.

Vegetative propagation has been a difficult challenge. Cuttings from tiny seedlings root readily, but rooting capability ceases before seedlings are 1 m (3 ft) tall because of natural rooting inhibitors produced by adult leaves *(32)*. However, even in adult trees, cuttings from epicormic shoots induced at the base of the tree by felling or girdling retain the ability to root. Rooting success varies substantially among clones, and there are strong seasonal influences and exacting cultural requirements for each geographic area. The technique is particularly advantageous in multiplying outstanding hybrid individuals. Starting in the mid-1970's, some commercial plantations were propagated by rooted cuttings in Brazil *(8,17)*, where the method is now used to establish major clonal plantations *(9)*. Reproduction through tissue culture techniques has also been demonstrated *(38)*.

Clonal seed orchards have been produced by grafting in South Africa, but delayed graft incompatibility is a common, debilitating problem. Incompatibility can be greatly reduced by grafting scions onto sibling or half-sibling rootstocks *(45)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth of rose gum on short rotations is rapid. Mean height growth of 2 m/yr (6.5 ft) is common *(29)*, and a rate of 4 m/yr (13 ft) has been reported *(35)*. Mean yields are about 27 m^3/ha/yr (386 ft^3/acre/yr) *(21)*. Wood increment on the best sites is even more impressive:

Country	Period	Yield	Reference
	(years)	*(m^3/ha/yr)*	
Colombia	4.5	25	*(24)*
India	8 to 10	20 to 25	*(31)*
South Africa	—	35	*(29)*
Uganda	—	17 to 45	*(29)*
Kenya	6 (coppice)	46	*(29)*
Brazil	7 to 8	45 to 73	*(35)*

Mean annual increment for height growth culminates early in Florida. On good sites, growth may average 3.5 m (11.5 ft) annually for the first 4 years, then taper off to average 2.4 m (7.9 ft) over an 8-year rotation. Adequately stocked commercial plantations have not reached harvest age, but preliminary growth data support the following planning assumptions:

An 8-year seedling rotation.

Trees averaging about 18 m (60 ft) tall at age 8 years.

Annual yield for volume and weight in the following range:

	Volume		Dry Weight	
	m³/ha	*ft³/acre*	*t/ha*	*tons/acre*
Pessimistic	12.9	184	5.4	2.4
Realistic	16.1	230	6.9	3.1
Optimistic	19.3	276	8.3	3.7

These indicated annual yields are well below world standards, and are probably due to south Florida's infertile soils and seasonally high water tables. Yields include about 18 percent bark by volume and 14 percent by weight. Density averages about 0.45 g/cm³ (0.026 oz/in³) for wood and about 0.32 g/cm³ (0.018 oz/in³) for bark. Moisture content is about 0.50 g/cm³ (0.029 oz/in³) for wood and 0.72 g/cm³ (0.042 oz/in³) for bark *(14)*.

Rooting Habit—Natural seedlings develop a pronounced taproot with few laterals if conditions permit. The roots of containerized seedlings more or less assume their natural form after being outplanted, regardless of previous restrictions *(3)*. Rose gum does not develop lignotubers *(6)*.

The soils of south Florida drastically sculpture the root systems of rose gum trees. These spodosols feature a thin, sandy A_1 horizon with meager accumulations of nutrients and organic matter. Below lies a strongly leached A_2 horizon of white, sterile sand. The A_2 changes abruptly to a B_2h, the spodic horizon, consisting of fine sand accreted with organic and aluminum compounds. In some areas this spodic hardpan perches water tables and resists root penetration both physically and by aluminum toxicity *(4)*. Typically, taproots penetrate about 50 cm deep (20 in), then divide into two or more smaller taproots that terminate barely into the spodic horizon *(4)*. Excavated trees show an abrupt fringe of dead lateral and feeder roots in the A_2 horizon, apparently anoxia mortality from perched or raising water tables during the summer rainy season *(4)*. This shallow anoxic zone restricts the exploitable soil during the prime summer growing season, and the roots cannot penetrate the spodic horizon to pursue the retreating water table during the long dry season.

Reaction to Competition—Rose gum is intolerant of shade. Seedlings can only develop in full or nearly full sunlight; trees must maintain a dominant or codominant canopy position to long survive. Suppressed trees quickly die and intermediate trees must grow to an overstory position or eventually lose vigor and die.

Despite their startling growth capacity, newly planted rose gum seedlings compete poorly with weedy vegetation, tolerating neither root competition nor shading. In Florida, they need 3 months reasonably free of competition to grow about 1.5 m (5 ft) tall and dominate the site. The local planting effort concentrates on virgin prairies and cutover pineland where chopping and bedding control the native ground cover sufficiently to permit rose gum establishment without post-planting weed control. However, early vegetative competition often retards growth and probably contributes to large tree-to-tree variation within stands. Post-planting weed control by herbicides and cultivation is beneficial *(37)*. An increase in volume at 5 years of 48 to 55 percent was obtained by combinations of cultivation and herbicide spraying during the first 24 months *(30)*. Competing vegetation also contributes to the fire danger. Rose gum completely occupies suitable sites in Florida with adequate stocking by plantation-age 2.5 years and herbaceous ground cover mostly disappears. On poor sites, intense competition may continue for 5 years.

Competitive relationships develop early among the plantation trees and stay well defined throughout the 8-year rotation. In Florida's first commercial plantation (fig. 1), 75 percent of the sample trees that were in the top quartile for height at age 2.5 years were still in the top quartile at age 8.5 years; and 73 percent of the trees in the bottom quartile at age 2.5 were either dead or still in the bottom quartile at 8.5 years. Similarly, out of 131 sample crop trees at 8.5 years, 85 percent had been predicted as crop trees at 2.5 years; of 37 sample trees that were culls or dead at 8.5 years, 68 percent had been predicted as culls at 2.5 years.

Damaging Agents—The greatest threat to rose gum survival is a lapse in soil moisture at outplanting time. If this occurs, managers must be prepared to stop planting until the rains begin again. Severe nursery losses have been suffered from a stem girdling fungal canker caused by *Cylindrocladium scoparium*, but alternating sprays of chlorothalonil and benomyl prevent or control it *(1)*.

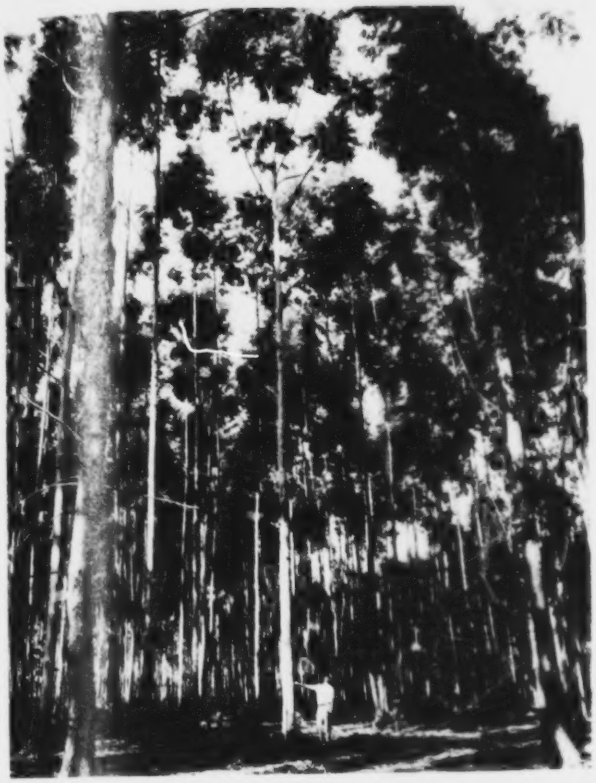

Figure 1—Eucalyptus grandis *in southwestern Florida, plantation age 7.5 years.*

Severe frost damages rose gum saplings even in the commercial plantation zone, but they sprout and regrow vigorously. Frost has cost a season's growth several times but never a plantation. South Florida usually has inversion freezes, with lower temperatures at ground level than at 2 m (6.6 ft). There is a strong positive correlation between freeze resistance and rapid early growth; resistant trees develop larger stems with thicker, insulative bark close to the ground, and also elevate tender terminal tissue into the higher, warmer air. Each additional year of growth reduces the risk of frost damage. Since planting research began in 1961, severe damage has been suffered 1 out of 3 years by seedlings in their first winter, 1 out of 5 years by saplings in their second winter, and only 1 out of 19 years by trees in their third winter or older.

Local plantations are suffering an increasing incidence of basal cankers caused by the fungus *Cryphonectria cubensis.* Canker incidence in the oldest pilot-scale plantation increased from 15 percent at age 7 to 50 percent at age 11 *(2).* Infected trees in Florida do not seem debilitated, but mortality has been serious in Brazil (30 percent) and Surinam (50 percent). Basal cankers may appear in trees less that 2 years old.

Lightning occurs with an unusually high frequency in southwest Florida *(36).* Over an 8.5-year rotation on a 67-ha (165-acre) plantation, 4.4 percent of the sample trees suffered lightning strikes or splashes and 2.5 percent actually died as a result.

No hurricane has struck southwest Florida since commercial planting began, but there is a 10-percent hurricane probability for any given year. A hurricane would cause serious windthrow, as hurricane Allen did to *Eucalyptus* in Jamaica *(41).*

Termites which devour seedlings during the first years, have been a serious problem in rose gum plantations in India *(28).* Also worth mentioning is the serious tendency of rose gum logs to end-split. Losses can be kept at a minimum by milling within 3 days of cutting, bucking to lengths as long as possible, and sawing carefully *(33).*

Special Uses

The sapwood of rose gum is pale pink and the heartwood light to dark red. The wood is straight grained, coarse textured, and moderately strong *(6).* It is moderately durable at best, but the sapwood is generally resistant to *Lyctus* spp. borers *(6,7).* The specific gravity varies from 0.62 to 0.80 *(6,7,23).* Rose gum timber is used for general construction, joinery, plywood, panelling, boat building, flooring, utility poles, mine timbers, and posts *(6,7).*

In 1972, rose gum wood harvested from an 8.5-ha (21-acre) research planting supported a commercial-scale trial run in a Florida pulpmill. A mixture of 70 percent rose gum and 30 percent native hardwood was manufactured into quality facial tissue with excellent properties of strength and softness *(42).* Earlier laboratory tests showed that debarked rose gum wood gave screened yields of kraft bleached paper pulp equal to those of representative native hardwood furnish at comparable kappa numbers. Brightness of bleached pulp was equal or superior to native hardwood controls at equivalent or slightly higher processing costs *(14).* However, strength properties of handsheets were generally inferior to those of native hardwood controls.

A pyrolysis test was conducted to determine the energy value that could be recovered from whole-tree chips of 9-year-old rose gum grown in southwest Florida. Seventy percent of the energy contained in the dry chips could be recovered as char and oil, which could be transported and stored. Twenty-one percent of the trees' energy value was converted to noncondensed volatile oil and low-energy gas that could only be used on site or sold to an adjacent user *(34)*.

Genetics

Rose gum is most closely related to *E. deanei* and *E. saligna (6)*. No subspecies or varieties are recognized.

Rose gum trees planted in southwest Florida constitute a land race developed through three generations of selection and progeny testing in the local environment. Because of recurrent selection for local adaptation, the trees perform better than progenies of outstanding trees selected in Australia, South Africa, or elsewhere.

A long-range breeding system calls for importing as many rose gum seed lots as possible—preferably collections from selected single trees in Australia—but some bulk lots and many lots from exotic populations outside Australia have been included. Each seed lot (family) contributes about 60 seedlings to a large outplanting called the genetic base population. All individuals of all families are completely randomized in single-tree plots. Trees are measured for growth rate and scored for cold hardiness, stem straightness, branch habit, and general adaptation. At 2.7 years (one-third of the rotation age), the trees are selected and the rest are rogued to convert the base population to a seedling seed orchard. The best families usually contribute three or four selects to the seedling seed orchard; most families contribute only one or two; and about one-third of the families drop out of the breeding population for lack of any worthy candidates.

Select trees exchange pollen in the first massive bloom at age 3+ years. The following spring the resultant seed is collected and used to establish the next generation's base population, which also is the progeny test of the seedling seed orchard. Thus, a generation of selection is completed in 4 years. Progeny test results identify the best commercial seed-orchard trees as well as poor seed trees to be rogued from the orchard.

Each generation of selection enhances the land race's adaptation to local conditions, but new families must be imported to broaden the genetic base and minimize inbreeding depression.

In the current genetic base population, first-generation Australian families average 7.5 dm^3 (0.26 ft^3) of stem volume at 2.5 years. Compared with those Australian families, second-generation Florida families average 95 percent more stem volume (14.6 dm^3 or 0.52 ft^3); third-generation families, 127 percent more (17.0 dm^3 or 0.60 ft^3); and fourth-generation families, 163 percent more (19.7 dm^3 or 0.70 ft^3).

A study designed to measure realized gain compares the following three populations, each in replicated block plantings:

> *Premier*—Six advanced-generation families (average 3.5 generations of selection) that are top-ranked for the combined traits of volume production, cold hardiness, form, and coppicing.
>
> *Commercial*—The 33 advanced-generation families (average 2.9 generations) included in the seed mix for the 1979 commercial season.
>
> *Ancestral*—Four imported seed lots from which all six premier families descend and 21 of the 33 commercial families.

At age 1.5 years both premier and commercial trees significantly exceeded the height of ancestral trees by 23 and 13 percent, respectively. The three populations all differed significantly in their cold hardiness. The premier families suffered mainly foliar damage, while the commercial and ancestral families suffered increasingly severe damage to foliage and woody parts.

Hybrids

The Florida land race is predominantly, but not purely, *E. grandis*. A few seed orchard trees and scattered offspring display recognizable admixtures of traits from *E. robusta, E. tereticornis*, and *E. camaldulensis*. Given synchronous flowering and proximity, rose gum can hybridize with many eucalyptus species. Some of the resultant F_1 hybrids are superior to either parent species for certain exotic forest environments, but F_2 and later generations show classic segregation and hybrid breakdown. F_1 hybrids between *E. grandis* and *E. tereticornis* seem especially promising in India *(43)* and Zambia *(16)*. In Espirito Santo, Brazil, hybrids between *E. grandis* and *E. urophylla* are planted as clonal stands from rooted cuttings *(8)*. In south Florida, there is evidence that F_1 hybrids between *E. grandis* and *E. robusta* could be more productive than either pure species.

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Eucalyptus robusta Sm. Robusta Eucalyptus

Myrtaceae Myrtle family

James P. King and Roger G. Skolmen

Robusta eucalyptus, *Eucalyptus robusta,* is native to a narrow coastal area in southeastern Australia. The species is widely adaptable and has been introduced into many tropical, subtropical, and warm-temperate climates including Puerto Rico, southern Florida, coastal California, and Hawaii. It is naturalized only in southern Florida and Hawaii. Commonly called swamp-mahogany in Australia, it is usually called robusta eucalyptus in the United States *(2,16),* and beakpod eucalyptus in Puerto Rico *(17).*

The species was originally introduced as a candidate for timber production, fuel, watershed protection, and windbreaks. By 1960, more than 4650 ha (11,500 acres) of plantations were established in Hawaii (fig. 1). The species has been studied in Florida as a source of pulpwood *(8).*

Figure 1—Robusta eucalyptus is used to produce sawtimber in Hawaii.

Habitat

Range and Climate

Robusta eucalyptus is native along the Australian coast of New South Wales and southeast Queensland. It is found mainly in swamps and on the edges of coastal lagoons and rivers where it is subject to periodic flooding *(5,9).* The mean maximum temperature in the hottest month is 30° to 32° C (86° to 90° F); the mean minimum of the coldest month is about 3° to 5° C (37° to 41° F). Throughout the native range, from 5 to 10 light frosts occur each year *(6).*

In Hawaii, robusta eucalyptus grows well from near sea level to 1100 m (3,600 ft) where annual rainfall ranges from 1000 mm (40 in) to 6350 mm (250 in) and temperatures rarely if ever reach freezing.

Robusta eucalyptus in Florida grows mainly in the southern portion of the State where frosts may occur annually. Mean annual rainfall averages 1320 mm (52 in) with 70 to 80 percent of rain falling during the May to October wet season.

In Puerto Rico the species makes its best growth in mountain regions about 460 m (1,500 ft) where annual rainfall averages 2540 mm (100 in) *(17).*

In southern California and along coastal northern California, plantings of robusta eucalyptus have been subject to several unseasonal cold spells *(11,20,21)* where temperatures reached -9° C (16° F). In every instance severe foliage damage was initially observed (more than 80 percent of the crown foliage killed), but the stems recovered within 3 months.

Although robusta eucalyptus can recover from occasional severe frost damage, the limiting variable in its distribution seems to be low temperature. If the temperature drops below -9° C (16° F) annually, introduced robusta eucalyptus will seldom be successful. In Yunnan Province, China, -7° C (19° F) damaged robusta eucalyptus, but to a lesser extent than *E. globulus (4).*

Soils and Topography

Robusta eucalyptus grows well on a variety of soils, ranging from its native intermittently flooded sites *(6,9)* to the hot summer-dry soils of California's Central Valley *(11).*

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In Florida, typical soils are poorly drained, acid, fine sands with hardpans at depths proportional to the depth of the seasonally high water table. Robusta eucalyptus does best on the least poorly drained of these soils, which are typical of arenic and aeric haplaquods of the order Spodosols *(7)*.

Most robusta eucalyptus in Hawaii are planted on sites considered too steep for agriculture—usually slopes of 10 to 20 percent. On the older islands of Kauai, Oahu, Molokai, and Maui, trees were planted predominantly on Oxisols and Ultisols. On the youngest island, Hawaii, plantings are mainly on Histosols and Inceptisols. All these soils are formed on basaltic parent materials, either volcanic ash or lava rocks. Soils are low in nitrogen and phosphorus and often strongly acidic. The lava substrate may be in either almost continuous sheets or in highly fractured porous clinkers. Soil drainage, therefore, varies from very poor to extremely rapid in very short distances.

Associated Forest Cover

In its native range the species is dominant in some areas and is often found in pure stands. Associated trees may include kinogum eucalyptus *(Eucalyptus resinifera)*, bloodwood eucalyptus *(E. gummifera)*, forest redgum eucalyptus *(E. tereticornis)*, longleaf casuarina *(Casuarina glauca)*, and various species of *Melaleuca (8)*.

Throughout the 1930's, when most of the tree planting was done in Hawaii, robusta eucalyptus was used to overplant failed plantations. Consequently, because robusta eucalyptus could survive on a wide variety of sites, it is found in many mixed plantings. Some common associates with robusta eucalyptus are saligna eucalyptus *(Eucalyptus saligna)*, tallowwood eucalyptus *(E. microcorys)*, melaleuca *(Melaleuca quinquenervia)*, horsetail casuarina *(Casuarina equisetifolia)*, and silk-oak *(Grevilla robusta)*. Treefern *(Cibotium* spp.) is also quite common in the understory of planted stands. One report refers to a pure stand of robusta eucalyptus being heavily invaded by Javanese podocarpus *(Podocarpus cupressina)*. On wetter sites on the island of Hawaii, robusta eucalyptus stands often develop a dense, almost impenetrable, understory of strawberry guava *(Psidium cattleianum)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Robusta eucalyptus has perfect flowers that are insect pollinated. In Florida, California, and Hawaii, trees have been observed to flower by the end of the third growing season. The peak flowering season in Florida is from September to November *(7)*, and the peak season in California is from January to March *(11)*. In Hawaii and more tropical areas, new flowers may appear at almost any time of the year and individual trees occasionally bloom year-round.

The trees flower with 5 to 10 flowered axillary umbels. The sepals and petals are fused into a caplike structure (operculum) that drops off the tip of the flower bud at anthesis. The eucalypts are, in general, protandrous *(23)*. The showy part of the cream-colored flower is actually the numerous filamentous stamens that surround the stigma.

The fruit is a vase-shaped dark green capsule 12 to 15 mm (0.5 to 0.6 in) long that contains many small seeds. The fruit ripens 5 to 7 months after flowering.

Seed Production and Dissemination—Seeds of robusta eucalyptus are small and like all eucalyptus contain no endosperm. The viable seed is difficult to separate from the chaff (unfertilized or aborted ovules) in the ripe flower capsules. There are 200 to 400 viable seeds per gram (5,700 to 11,300/oz) of seed and chaff *(12)*.

Seed dispersal is largely by wind and may begin within 6 weeks after the seed capsule ripens. In Florida, most trees retain seeds in closed capsules for more than 1 year after ripening *(7)*.

Seedling Development—Germination is epigeal *(12)*. Robusta eucalyptus in Florida has occasionally reproduced naturally around abandoned homesteads, probably following fire on the native range. The seed source was usually an old amenity planting of robusta eucalyptus and the seedlings outgrew the disturbed native vegetation. The species does not invade recently abandoned agricultural fields because of the more intense competition from weeds *(7)*.

Most robusta eucalyptus stands in Florida are being established through the planting of container-grown stock. Seedlings in Florida need several months to grow into frost-hardy saplings before facing their first frost. Early spring planting would be ideal, but soil moisture is deficient until summer rainfall begins. Thus mid-June through mid-August is the recommended planting period *(7)*.

Most robusta eucalyptus stands in Hawaii have been established as single species plantings and, after logging or other disturbance, regenerate as pure stands of coppice and seedlings. Robusta eucalyptus has recently been used in biomass plantations. These were all made with container-grown seedlings to assure the rapid early start needed to stay ahead of the wide variety of competing, aggressive vegetation *(25)*. After planting, container-grown seedlings in Hawaii grow almost 30 cm (12 in) per month for the first few years.

Vegetative Reproduction—The majority of new stems in logged stands of robusta eucalyptus are of coppice origin. These coppice shoots arise from dormant buds in the cambium of the stump. All parts of the stem surface under the bark contain dormant buds that sprout rapidly after crown injury.

Robusta eucalyptus is one of the *Eucalyptus* species that produces lignotubers. A lignotuber consists of a mass of vegetative buds and contains substantial food reserves. It begins forming in the axils of the cotyledons and the first three pairs of the seedling leaves. Eventually these organs are overgrown by the main stem and remain as tuberous bulges just above the root crown.

When robusta eucalyptus is logged, therefore, the source of the coppice is usually the dormant buds in the stem cambium surrounding the stump. But if the entire stem is killed through fire, or in young seedlings through grazing, new coppice shoots may arise from the lignotubers *(23)*. In a Florida test, robusta eucalyptus coppicing proved to be less influenced by season of cutting than either *E. grandis* or a hybrid *E. grandis* × *robusta*, but was reduced during the hot, dry summer *(26)*.

No rooted cuttings of robusta eucalyptus have been used on a commercial scale, but cuttings taken from young seedlings and young coppice shoots have been successfully rooted *(10)*.

Sapling and Pole Stages to Maturity

Growth and Yield—In 1960, a study in eight different Hawaiian plantations of robusta eucalyptus gave the following growth data for plantations at elevations ranging from 395 to 730 m (1,300 to 2,400 ft), and trees aged 23 to 38 years, with 358 to 642 trees per hectare (145 to 260/acre) larger than 28 cm (11 in) in d.b.h. *(14,22)*:

Basal area: 51 to 184 m²/ha (220 to 800 ft²/acre).
Height of dominants: 28 to 55 m (93 to 179 ft).
Mean annual growth per stand: 7 to 48 m³/ha (100 to 685 ft³/acre).
Mean annual growth for all eight stands: 26 m³/ha (370 ft³/acre).

One of Florida's first eucalyptus plantations of operational scale established with genetically improved seedlings was established in 1972 on a palmetto prairie site. Within this planting, a system of inventory plots was established to develop the data needed to determine optimum rotation length, expected yields, and other management guidelines. Although the planting is considered seriously understocked with 786 trees per hectare (318 trees/acre), measurements at 10.25 years estimate a mean annual yield of 16.7 m³/ha (238 ft³/acre). Mean height of all stems was 16.6 m (54.5 ft) and height of dominant class trees only was 21.3 m (70 ft). Stand volume in 1979 was 172 m³/ha (2,458 ft³/acre) *(7,18)*.

Planted trees in Puerto Rico have reached 27.4 m (90 ft) in height and 41 cm (16 in) in d.b.h. in 15 years *(17)*. Coppice stands often outproduce seedling stands. A 10-year-old coppice stand in Hawaii produced 140 m³/ha (2,000 ft³/acre), while an adjacent 12-year-old seedling stand yielded only 96 m³/ha (1,372 ft³/acre) *(3)*.

Rooting Habit—The most distinctive characteristic of the rooting habit of robusta eucalyptus in Hawaii is the tree's ability, in moist areas, to initiate adventitious roots from buds on the stem at heights of 6 to 12 m (20 to 40 ft) (fig. 2) *(13)*. These roots grow downward through the moist bark and into the soil. As the root grows in diameter, it sometimes breaks free from the soft bark and appears as an aerial root. The lower stems of occasional robusta eucalyptus become completely encased in an interwoven mass of these aerial roots, some of them 20 cm (8 in) in diameter *(14)*. The species rarely displays this habit in its native range or in more temperate climates. Adventitious roots, however, have been noted on a robusta eucalyptus in the Sydney Botanical Garden in Australia, and near Rio de Janeiro *(15)*. Although some layering from the stem may occur as noted earlier, most roots originate below the lignotubers and occupy the entire available soil profile on well-drained sites. Robusta eucalyptus is usually quite windfirm on deeper soils and is often used for windbreaks in Hawaii.

Reaction to Competition—Robusta eucalyptus is classed as intolerant of shade. Where planted in alternate rows with saligna eucalyptus it is invariably overtopped, suppressed, and usually dies within 30 years. In Hawaii, robusta eucalyptus is planted on prepared sites and usually grows faster than weedy competitors invading the site. On extremely refractory sites robusta eucalyptus is considered the species of last resort because of its remarkable ability to survive and grow.

Damaging Agents—Robusta eucalyptus is remarkably free of serious insects or diseases when grown in the United States. *Cylindrocladium scoparium* has caused serious losses of seedlings in Florida *(1)*. However, this fungus can now be successfully controlled by fumigation of soil and containers with methyl bromide before sowing and a followup treatment with benomyl spray. The major cause of damage to robusta eucalyptus stands in Hawaii is wind *(14)*. Violent windstorms have snapped stems and uprooted trees. Uprooting damage can be particularly severe when stands are established in shallow soils overlaying a solid mantle of lava rock. Naturally, such shallow soils should be avoided and planting concentrated on soils or fractured bedrock where roots can penetrate to greater depths.

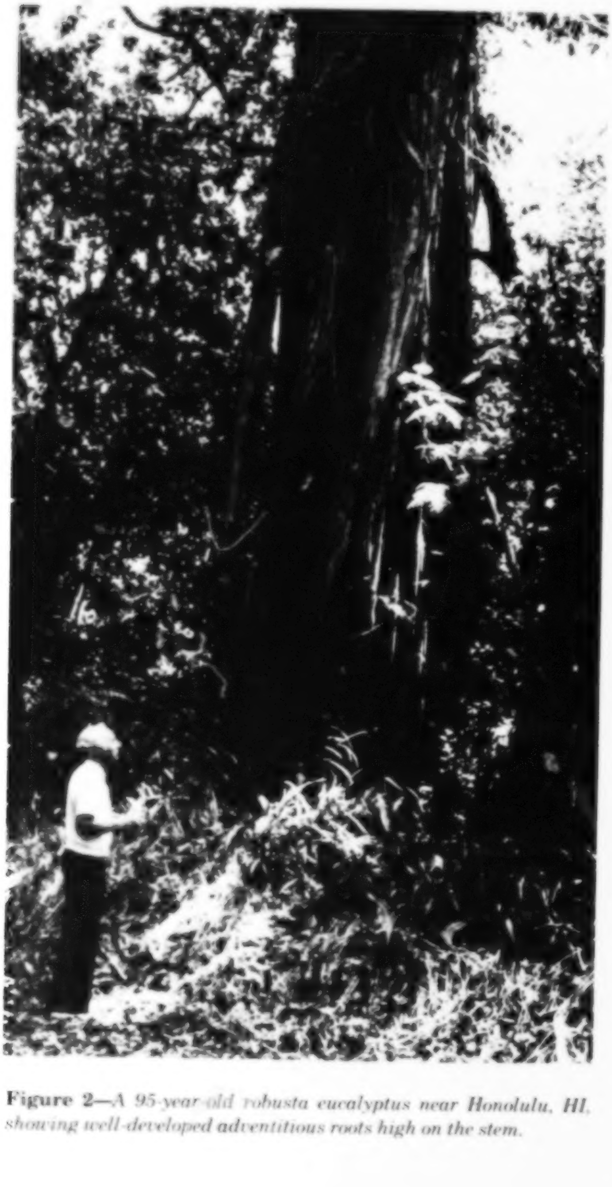

Figure 2—*A 95-year-old robusta eucalyptus near Honolulu, HI, showing well-developed adventitious roots high on the stem.*

In Florida, robusta eucalyptus plantings at about age 5 may develop a condition called "robusta breakup." Patches of young trees may develop a bend in the main stem or on primary branches. Breakage may also occur along the main stem or primary branches, and the wood at the point of breakage may appear dry and brash. No primary pathogens or pests have been associated with this breakage. Minor element deficiencies are suspected but are not proven as the cause. Adjacent stands of rosegum eucalyptus *(Eucalyptus grandis)* appear unaffected *(7)*.

Special Uses

Robusta eucalyptus has found use in urban forestry and as farm windbreaks because of its dark shiny leaves and its generally dense crown. Twigs and branches continually die off and fall to the ground, however, so that the tree is rather hazardous for use in parklands, campgrounds, or even gardens. On the island of Kauai, an older roadside planting of robusta eucalyptus, though most attractive, is maintained at a high cost for road cleanup.

Genetics

Population Differences

We know of no published data on population differences in robusta eucalyptus. Studies (see "Races") using seed collections from Australia could be suitable for grouping and analyzing by particular provenances, but such analyses have not been reported.

Races

In 1975, foresters in southern Florida established a genetic base population of 352 collections of *Eucalyptus robusta* from individual selected trees in Australia, advanced generation families from two previous generations of selection in Florida, as well as selections from Florida's naturalized stands. This base population was subsequently selected and rogued to form a seedling seed orchard that produces seeds of a *bona fide* land race of *E. robusta* for southern Florida. This seed orchard was also a source of genetic material for an effort to develop *E. grandis* and *E. robusta* hybrids adapted to Florida conditions *(7, 19)*.

Hybrids

Several natural hybrids involving *Eucalyptus robusta* have been reported *(24)*. All of the known interspecific hybrids are between *E. robusta* and other species of the subgenus *Symphomyrtus*. Several have been assigned recognized botanical names. They are *E. botryoides* var. *platycarpa* (*E. botryoides × robusta*), *E. grandis* var. *grandiflora* (*E. grandis × robusta*), *E. longifolia* var. *multiflora* (*E. longifolia × robusta*), *E. kirtoniana* (*E. robusta × tereticornis*), *E. patentinervis*, *E. insizwaensis* (*E. robusta × globulus*, probably), and an unnamed hybrid (*E. robusta × saligna*, probably).

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Eucalyptus saligna Sm. Saligna Eucalyptus

Myrtaceae Myrtle family

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Saligna eucalyptus *(Eucalyptus saligna)*, also called Sydney bluegum, is a fast growing tree, valuable in plantation forestry. It grows in several warm temperate to subtropical countries, such as Brazil and the Republic of South Africa, and the state of Hawaii.

The name *Eucalyptus saligna* was given to type specimens in 1797. Another very similar but distinct species, found within the same geographic range, *Eucalyptus grandis*, was not named until 1918 *(12)*. Before 1918, many introductions were made worldwide of seed collected from *"E. saligna"* that bore the characteristics of the type later to be called *E. grandis*. In most countries where introductions were made, therefore, considerable mixed planting and hybridization of the two species are present. Thus, in Hawaii, most saligna eucalyptus stands contain trees with a range of characteristics intermediate between those of *E. saligna* and *E. grandis*. *Eucalyptus grandis* is now preferred in South Africa because it self-prunes more readily and has smaller branches *(28)*; and in Brazil because it is resistant to a canker disease and can be propagated vegetatively *(6)*. *Eucalyptus saligna* has grown well where the climate is cooler; for example, in northern New Zealand *(12)* and in the uplands of Hawaii. Recent provenance tests of the two species in Hawaii suggest that *E. grandis* would be a better choice than *E. saligna* for most sites *(26)*.

Habitat

Native Range

Saligna eucalyptus is native to the east coast of Australia from Bateman's Bay (lat. 36° S.) in southern New South Wales to the southeastern corner of Queensland (lat. 27° S.) *(13)*. In the United States, it has been introduced into Florida, California, and Hawaii. In Hawaii it reproduces at the edges of planted stands. Although it was introduced into Hawaii in the late 1800's, the tree was not planted extensively until the 1960's, when it became the principal tree used for forestation.

Climate

In Australia, the tree grows from sea level to 30 m (1,000 ft) in the South and to 1220 m (4,000 ft) i the North. The climate within this range is warm temperate to subtropical, with winter frosts to –15 C (5° F) at the higher elevations *(12)*. In Ne Zealand, seedlings were frost tolerant to a minimum temperature of –7° C (21° F) *(21)*. Rainfall is evenl distributed, or has a summer maximum, and range from 890 to 1270 mm (35 to 50 in) annually *(13)*.

In Hawaii, saligna eucalyptus grows well betwee elevations of about 150 m (500 ft) and 1100 m (3,60 ft) where the temperature is never below 4° C (40 F). One stand is at 1980 m (6,500 ft) where ligh winter frosts occasionally occur, and the averag daytime temperature is about 16° C (60° F). Most o the saligna eucalyptus stands have been planted between 300 and 610 m (1,000 and 2,000 ft) elevatio in locations with evenly distributed or winter maximum rainfall of 1520 to 7620 mm (60 to 300 in annually. The tree achieves its best growth on site with about 2540 mm (100 in) annual rainfall, rathe than on wetter sites, possibly because sunlight i greatly reduced by the cloud cover on wetter sites.

Soils and Topography

In the northern part of its range in Australia saligna eucalyptus extends to the slopes and ridges In northern New South Wales and Queensland, it i usually on the slopes, while the closely relatec rosegum eucalyptus *(Eucalyptus grandis)* is usually near or at the valley bottoms. Saligna eucalyptus does best on clay loams derived from shales and requires good drainage *(13)*.

In Hawaii, saligna eucalyptus has been planted extensively on Histosols and Inceptisols on the island of Hawaii, and also on the Oxisols and Ultisols o Maui, Molokai, Oahu, and Kauai. These soils have in common moderate to strong acidity, low to very low available nitrogen and phosphorus, and rapid to very rapid drainage. All are formed on basaltic parent material, either volcanic ash or rock. In other respects they differ considerably, but all are unsuited or only marginally suited for agriculture. Slopes are usually 10 to 20 percent.

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Associated Forest Cover

In Australia, saligna eucalyptus is usually found in mixture with tallowwood eucalyptus *(Eucalyptus microcorys)* and blackbutt eucalyptus *(E. pilularis)*, the main coastal species of New South Wales, and is also found associated with several other eucalypts. It seldom grows in pure stands, whereas the closely related rosegum eucalyptus is typically found in pure stands *(13)*. The common names used follow those of Bryan and Walker *(2)*.

In Hawaii, saligna eucalyptus has been planted in mixture with three species of eucalyptus—tallowwood, robusta *(Eucalyptus robusta)*, and rosegum—with melaleuca *(Melaleuca quinquenervia)*, Formosa koa *(Acacia confusa)*, horsetail casuarina *(Casuarina equisetifolia)*, silk-oak *(Grevillea robusta)*, and a host of other species. On most sites, it has outgrown and shaded out or badly suppressed all of these species except the equally fast growing rosegum eucalyptus and the tolerant Formosa koa. In closed stands, about the only understory species found are strawberry guava *(Psidium cattleianum)* and occasional treefern *(Cibotium* spp.).

Life History

Reproduction and Early Growth

Saligna eucalyptus grown in Hawaii regenerates naturally on bare soil immediately after logging, or on cultivated land adjacent to planted stands. It rarely becomes established in undisturbed grass or brush cover and never in its own shade. Coppicing of stumps is variable. Usually about half to two-thirds of the stumps will sprout *(26)*. Age, weather, and (probably) heredity influence coppicing. The tree also usually produces a mass of special bud tissue at the groundline known as a lignotuber. The lignotuber will sprout if the stem is killed back by fire or other injury.

Flowering and Fruiting—Saligna eucalyptus trees begin to flower at 3 to 4 years of age. Flowering in Hawaii is most prolific during January to March but occurs to some extent year round. In Australia, the tree also flowers from January to March; in California, from April to June. Flowers that consist of numerous stamen filaments surrounding a single shorter pistil occur in umbels of 4 to 9 flowers. Before opening, the flower buds are about 10 mm (0.4 in) long and 5 mm (0.2 in) in diameter with a short stalk (pedicel), and a blunt, rather pointed cap (operculum) enclosing the stamens. Flowers are perfect. The opened flowers are yellowish white and are insect pollinated. Pollen is generally shed before the style becomes receptive, so selfing is rare.

The fruit is a dark-brown, bell-shaped capsule 0.8 cm (0.3 in) long and 0.5 cm (0.2 in) in diameter. It is short stalked and has four pointed, rim level, or slightly exserted valves. The capsule ripens about 6 months after flowering but opens to release seed 1 or 2 months after ripening *(12,13,20)*.

Seed Production and Dissemination—Seeds are black, irregularly shaped, and about 1.3 mm (0.05 in) in diameter. They are released along with a large amount of reddish-brown chaff when the capsule valves open. There are 460 viable seeds per gram (13,000/oz) of seed plus chaff *(20)*.

Seeds are naturally dispersed by wind. They can be collected from ripe capsules dried to open after picking. Some unopened ripe capsules are always present on trees in Hawaii but are most common in August and September. Fresh seeds germinate readily in 10 to 20 days without pregermination treatment. Seeds can be stored in airtight containers for several years at 0° to 5° C (32° to 41° F) *(20)*.

Seedling Development—The seedling has obcordate (inverse heart-shaped) cotyledons that are borne epigeously as in all eucalypts. Juvenile leaves are opposite for 3 or 4 pairs, then become alternate, short stalked and lanceolate, and 2.5 by 5.0 cm (1 by 2 in) in size. The adult leaves are alternate, stalked and lanceolate, tapering to a long point, 2.3 by 15 cm (1 by 6 in) in size *(13)*.

In Hawaii, nursery-grown seedlings in containers reach plantable size in 4 to 5 months. Although seedlings are hardy and will survive bare or open-rooted planting, planting of container-grown stock provides more assurance of success if the weather is dry just after planting. Under adverse conditions newly planted seedlings often desiccate and suffer leafdrop, but such plants usually sprout from the lower stem and recover. When this dieback slows growth, additional weeding or maintenance usually is required to clear competition *(32)*.

Around the world, seeds usually are germinated in flats containing light-textured medium, and seedlings are transplanted into other containers after 6 to 8 weeks when a third pair of leaves begins to appear *(12)*. Seeds also are sown directly into beds or tubes, but thinning of seedlings is usually required with this method because the small seeds are difficult to handle individually. Thinning requirements can be overcome by using pelletized seed and seeding devices *(15,31)*.

In Hawaii, saligna eucalyptus seedlings have been grown extensively in open beds. Because of their rapid growth, these seedlings usually are root pruned at 15-cm (6-in) depth at 6 months and top pruned at 8 months to a 30-cm (12-in) height. Bare root stock frequently has not survived well after field planting, and Hawaii's practice has now changed to growing seedlings only in polyethylene tubes *(30)*.

On favorable sites in Hawaii, planted seedlings grow to about 3 m (10 ft) in height in 1 year, and 3 to 5 m (10 to 16 ft) per year for the next 10 years. After clear cutting of a 44-year-old saligna eucalyptus plantation, natural seedlings that became established grew to saplings that averaged 9 cm (3.5 in) in d.b.h., and 11 m (36 ft) in height, 22 months after logging. Several of these saplings were 18 m (59 ft) tall.

Vegetative Reproduction—Saligna eucalyptus can sprout prolifically from dormant buds located in the cambium throughout the stem. After a tree is cut, shoots sprout from many points on the remaining bark surface. Those highest on the stump suppress those lower down and, if not broken off by wind or by weak attachment, become coppice stems that overgrow the stump *(12)*.

Sprouts will also grow from the lignotuber, a mass of bud tissue at or just below the groundline. Lignotubers are found on saligna eucalyptus from all but its northernmost provenances, but not on rosegum eucalyptus *(12)*. In managing saligna eucalyptus for coppice, it is desirable to cut stumps 12 cm (5 in) or less in height, so that the sprouts will develop from near the lignotuber. Such sprouts generally are more firmly attached but are frequently suppressed by sprouts arising from higher on the stump. Lignotubers persist when stems are killed by shading, thinning, or fire and often sprout vigorously after a mature stand is cut *(8)*.

Rooting of cuttings of saligna eucalyptus had been difficult *(16)* until a method was developed at the Aracruz Co. in Brazil *(7)*. The method consists of collecting coppice sprouts that are just beginning to harden and keeping them constantly moist while 2-leaf-pair cuttings are prepared and end-dipped in rooting hormone. The cuttings are placed under intermittent mist in individual containers. In Hawaii, saligna eucalyptus has been easier to root than *E. grandis*, although most success elsewhere has been with *E. grandis (3,7)*. However, just as was found for *E. grandis* in Brazil *(6)*, cutting rootability is variable among coppice from individual saligna eucalyptus trees.

Tissue culture propagation has also been successful in Hawaii. The techniques used with saligna eucalyptus are essentially those reported by Boulay *(1)* for other eucalyptus species. Terminal and lateral shoot tips of greenhouse-grown rooted cuttings are multiplied, separated, and rooted in sterile culture, and afterwards grown to normal size in a mist chamber. A number of propagules of saligna eucalyptus produced by tissue culture are now being compared in clonal progeny tests.

Grafting success has been reported for saligna eucalyptus *(24,27)*. Cleft, side, splice, and bottle grafting were all used successfully, but the tests were not observed for a long enough period to determine the extent of long-term incompatibility, a problem with many species of *Eucalyptus*.

Sapling and Pole Stages to Maturity

Growth and Yield—Saligna eucalyptus is a fast growing tree, well suited for producing high yields of wood fiber on short rotations (fig. 1). Measurements of a plantation spacing study on a good site at Kaumahina, Maui *(29)* provide an example. Four spacings were tested: 2.4 by 2.4 m, 3.0 by 3.0 m, 3.7 by 3.7 m, and 4.3 by 4.3 m (8, 10, 12, and 14 ft). At 2 years, trees averaged 9.6 cm (3.8 in) in d.b.h. and 10.7 m (35 ft) in height. At 5 years, they had grown to 20.8 cm (8.2 in) in d.b.h. and 22.9 m (75 ft). Mean annual volume increment had already peaked at the two closer spacings in the study and was rapidly leveling out at the wider spacings. At 15 years, the trees in this study averaged 26.7 cm (10.5 in) in d.b.h. and 39 m (129 ft) tall. The largest tree was 61 cm (24 in) in d.b.h. and 49 m (161 ft) tall. At 5 years, the trees at 2.4 by 2.4 m (8 by 8 ft) had produced 294 m^3/ha (4,200 ft^3/acre), or 58.8 m^3/ha (840 ft^3/acre) per year. At 15 years, these trees yielded 683 m^3/ha (9,759 ft^3/acre), or 45.6 m^3/ha (651 ft^3/acre) per year. Trees at 4.3 by 4.3 m (14 by 14 ft) yielded 33.1 m^3/ha (473 ft^3/acre) per year.

These figures are comparable to those of *Eucalyptus grandis*/*E. saligna* grown in other countries. In Kenya, a mean annual increment over 5-year periods of 21 m^3/ha (300 ft^3/acre) for the seedling crop followed by 32 m^3/ha (457 ft^3/acre) for the first coppice crop was obtained *(11)*. Other mean annual increment figures cited for *E. grandis* are 14 to 45 m^3/ha (200 to 643 ft^3/acre) in Uganda, 28 m^3/ha (400 ft^3/acre) in Zambia, 50 m^3/ha (715 ft^3/acre) at 14 years in Argentina, and 22 m^3/ha (314 ft^3/acre) in New South Wales, the native habitat of both species *(12)*.

In two 4-year-old stands in Hawaii, annual increment averaged 13 and 36 m^3/ha (185 and 515 ft^3/acre). The faster growing stand yielded wood with a specific gravity of 0.41 for an estimated annual dry-weight yield of stem wood of 15 tonnes/ha (6.7 tons/acre).

The tallest tree in Hawaii, thought to be the tallest hardwood in the United States, is a saligna eucalyptus. When last measured in 1979, the tree was about 50 years old, 137 cm (54 in) in d.b.h. and 82.3 m (270 ft) tall.

Rooting Habit—Saligna eucalyptus develops roots throughout the soil profile so that it is quite windfirm on deep soils, but easily windthrown on shallow soils. It does not produce a taproot. Roots are primarily from the stem below the lignotuber, although layering sometimes occurs a short distance from the lignotuber on buried stems. In plantations in Hawaii that are not subject to periodic short drought, about two-thirds of the root system is confined to the upper 61 cm (24 in) of soil where most of the available nutrients are found. In plantations subject to occasional drying of the surface soil, the shallow roots are killed and a deeper root system develops.

Reaction to Competition—Because the tree is such a fast starter, planted seedlings can frequently grow faster than surrounding grass and herbaceous vegetation and shade it out. This is particularly true if the seedlings have an intact root system when planted, as in modern tube container planting, so that little or no "shock" occurs to delay new growth after planting. At the upper elevational boundaries of sugarcane fields, saligna eucalyptus grown from seed in the soil at the time of cane harvest actually outgrew the sugarcane ratoon crop.

In Hawaii, original plantings are made on completely cleared land. Pre-emergent herbicides, though effective, have rarely been used. If pre-emergents are not used, one cleaning around trees that require it is made after 3 months and, depending on the site, a second cleaning may sometimes be made at 6 months. Further weeding is seldom necessary. Coppice growth of saligna eucalyptus is so rapid that competing plants are rarely a problem after cutting.

Tests in Hawaii show that the leguminous tree *Albizia falcataria* outgrows saligna eucalyptus on some sites when planted row on row with both species equally fertilized. It is one of the few woody plants known that can grow this fast on sites that are suited for saligna eucalyptus. The trials of mixing the legume with *E. saligna* produced increased yields of the eucalypt on some wet sites, but reduced yields on other, drier sites *(10)*.

In South Africa, thinning schedules have been developed for trees planted at 1330/ha (538/acre) that call for thinning 25 percent of the stems present at 6 years when the stems removed are 13 cm (5 in) in diameter, and 25 percent again at 10 years when they are 20 cm (8 in) *(12)*. These thinnings are continued at 3- to 5-year intervals until a sawtimber harvest is made at age 30. In the interim, all stumps are allowed to coppice to keep the site free of competition and to supply fuelwood crops.

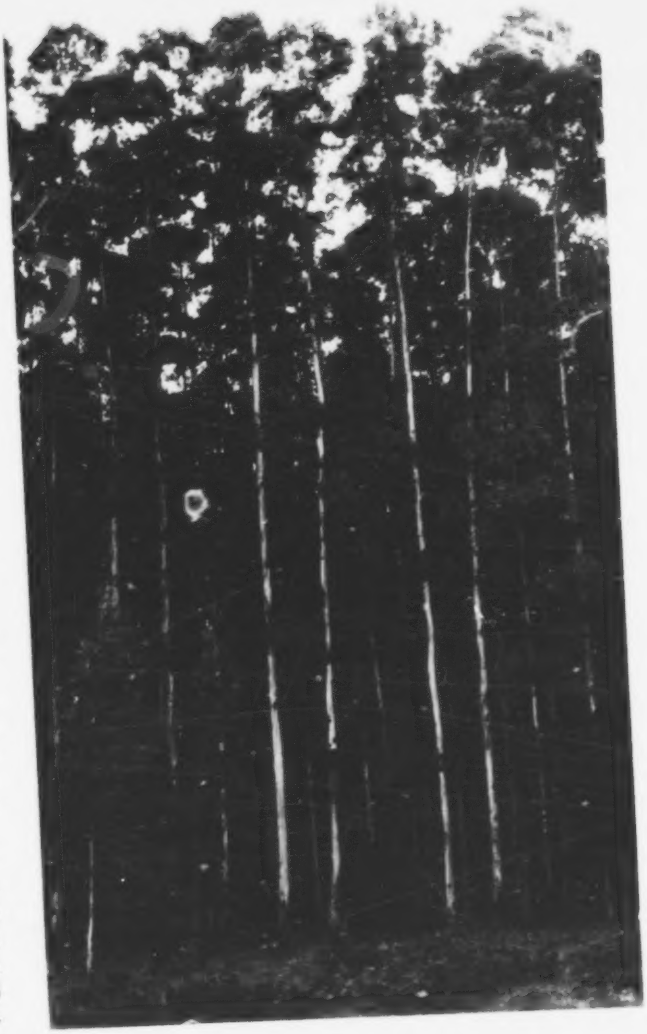

Figure 1—*Saligna eucalyptus stand at Kainehe, Island of Hawaii. At 32 years, this stand contained 1425 m³/ha (20,358 ft³/acre), mean annual growth was 44.5 m³/ha (636 ft³/acre), and average height of dominant trees was 59.7 m (196 ft).*

Saligna eucalyptus is classed as very intolerant of shade and the slower growing trees in a stand quickly become suppressed. In Hawaii, crown closure is usually complete and crown differentiation begins in

3 years in stands planted at 3 by 3 m (10 by 10 ft). In coppice stands where numerous stems grow from every stump, crown differentiation begins as soon as sprouts appear. Many studies have shown that the maximum yield of wood is obtained by not thinning coppice at all *(12)*. However, if larger diameter and straighter stems are desired, thinning to one to three stems per stump is desirable.

Damaging Agents—Saligna eucalyptus grown in plantations in many parts of the world is susceptible to the eucalyptus canker disease, *Cryphonectria cubensis*. The disease kills young trees, deforms stems, and causes basal cankers that reduce the coppicing ability of stumps *(19)*. Rosegum eucalyptus is somewhat resistant and *Eucalyptus urophylla*, perhaps, is immune to the disease, so these species are now being used in place of *E. saligna* in many Brazilian plantings. In Hawaii, the disease is present only on the island of Kauai. It attacks *E. grandis* in Florida but is not causing serious damage *(18)*.

In Western Australia, two other canker diseases, *Botryosphaeria ribis* and *Endothia havaensis*, were determined to be pathogenic on *E. saligna* planted there, while another, *Cytospora eucalypticola*, was present but less damaging *(14)*.

Phoracantha semipunctata, a wood-boring insect, degrades wood and reduces growth of eucalyptus in many places, including Hawaii, but is only a serious problem in trees that are stressed by severe drought. In Australia, saligna eucalyptus is subject to damage by *Spondyliaspis* psyllids, which predispose the trees to attack by the wood-boring beetle *Xyleborus truncatus (22)*.

In Hawaii, wind damage is a severe problem. In January 1980, a severe windstorm caused severe blowdown in 75 percent of the saligna eucalyptus stands planted during the 1960's *(17)*.

Special Uses

In Hawaii, saligna eucalyptus has been used to some extent for sawtimber, but only with considerable difficulty and expense. Most of the milling and lumber quality problems are those associated with growth stress—severe end-splitting of logs, spring of cants during sawing, compression failures, and brashness of the wood near the pith *(25)*. Because of this, the tree is now planted primarily for early harvest as pulpwood, or, if it proves economic in the near future, as industrial fuelwood to replace oil.

Elsewhere in the world, particularly in South Africa and Brazil, the trees and their close relative, *E. grandis*, are grown extensively for pulp, poles, and fuel.

Genetics

Population Differences

In an attempt to solve the problem of confused and probably mixed introductions of *Eucalyptus saligna* and *E. grandis*, differences between them have been noted for mature trees in South Africa *(12)*, as follows:

E. saligna	*E. grandis*
Bark: Smooth type bluish; rough type only on lower stem	Smooth type white; rough type often extends up stem
Flowering (South Africa): January to April	July to December
Valves of fruit: 3 or 4 pointed, straight or spreading	4 to 6 blunt, incurved
Root crown: Lignotuberous	Not lignotuberous
Branches: Persistent under shade	Not persistent under shade

These characteristics vary among provenances of each species. The northernmost provenances of saligna eucalyptus, for example, do not have lignotubers *(12)*. When grown in some locations, for example, Hawaii, flowering seasons overlap and trees probably hybridize extensively. Among 6-year-old trees of provenances collected in Australia growing side-by-side at two locations in Hawaii, no consistent differences were observed between *E. saligna* and *E. grandis* in leaves, bark, or branching habit *(26)*.

Saligna eucalyptus produces denser wood than *E. grandis*, but in Hawaii *(26)*, and also in the Republic of South Africa *(9)* where yields of the two species growing on the same sites have been compared, the best performing *E. grandis* provenances for a particular site produce a higher total weight yield than *E. saligna*, despite the wood density difference.

Hybrids

Because of the wide international interest and the problems of hybridization and identification of the two species, a comparison of *E. saligna* and *E. grandis* populations representative of the entire range of each species was made in Australia *(4)*. Distinct differences were found in seedling and mature-tree morphology and allozyme frequencies between core populations of the two, but intermediate types were found in some remote locations. Core mature saligna eucalyptus had smaller seed, upright valves (4 per fruit), and non-glaucous fruit and branchlets as compared with *E. grandis*, which had larger seed, incurved valves in 5's, glaucous fruit and branchlets. Saligna eucalyptus seedlings had lignotubers and were glaucous; not so, *E. grandis*. Saligna eucalyptus seedlings also had smaller cotyledons and narrower, longer leaves. The allozyme patterns found for native populations in Australia showed species differences and were later compared to patterns found for populations collected in the Republic of South Africa, which were thought to be hybridized *(5)*. All the South African trees sampled fell within the allozyme patterns found in Australia for *E. grandis*, even though several were morphologically suspect.

In addition to the *Eucalyptus grandis/E. saligna* complex, *E. saligna* crosses with *E. robusta*, bangalay eucalyptus *(E. botryoides)*, and probably with forest redgum eucalyptus *(E. tereticornis) (12,28)*. In the southern part of its natural range, a region of introgression of *E. saligna* with *E. botryoides* exists *(23)*.

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Fagus grandifolia Ehrh. American Beech

Fagaceae Beech family

Carl H. Tubbs and David R. Houston

American beech *(Fagus grandifolia)* is the only species of this genus in North America. Although beech is now confined to the eastern United States (except for the Mexican population) it once extended as far west as California and probably flourished over most of North America before the glacial period *(39)*. This slow-growing, common, deciduous tree reaches its greatest size in the alluvial soils of the Ohio and Mississippi River Valleys and may attain ages of 300 to 400 years. Beech wood is excellent for turning and steam bending. It wears well, is easily treated with preservatives, and is used for flooring, furniture, veneer, and containers. The distinctive triangular nuts are eaten by people and are an important food for wildlife.

Habitat

Native Range

American beech (fig. 1) is found within an area from Cape Breton Island, Nova Scotia west to Maine, southern Quebec, southern Ontario, northern Michigan, and eastern Wisconsin; then south to southern Illinois, southeastern Missouri, northwestern Arkansas, southeastern Oklahoma, and eastern Texas; east to northern Florida and northeast to southeastern South Carolina. A variety exists in the mountains of northeastern Mexico.

Climate

Within the range of beech, annual precipitation usually is from 760 mm to 1270 mm (30 to 50 in) *(39)*; however, some beech is found in Michigan where precipitation is about 580 mm (23 in), and in Canada where about 640 mm (25 in) fall annually. Precipitation during the growing season varies from 250 mm to 460 mm (10 to 18 in). Beech is a mesophytic species; it uses twice as much water for transpiration and growth processes annually, compared to some drought resistant oaks and even lesser amounts by some pines.

The growing season for beech varies from 100 to 280 days; the species is found in one county in Michigan where the growing season is only 92 days. Mean annual temperatures range from 4° to 21° C (40° to 70° F). Beech can exist under temperature extremes lower than -42° C (-44° F) and 38° C (100° F). Higher than average summer temperatures may be unfavorable for beech growth.

Soils and Topography

Beech is found generally within two principal soil groups: the gray-brown podzolic (Hapludalf) and the laterite (Acrorthox) and is prevalent on podzols; it is seldom found on limestone soils except at the western edge of its range. These soils are contained in the orders Alfisols, Oxisols, and Spodosols. Soils of loamy texture and those with a high humus content are more favorable than lighter soils *(39)*. The largest trees are found in the alluvial bottom lands of the Ohio and the lower Mississippi River valleys, and along the western slopes of the southern Appalachian Mountains.

Beech populations frequently are higher on coarse-textured, dry-mesic soils in the northern part of its range *(38)*. In Indiana, beech is more sensitive to reduced soil moisture than is white oak *(Quercus alba)*, sugar maple *(Acer saccharum)*, American elm *(Ulmus americana)*, and slippery elm *(U. rubra)*. It will grow on poorly drained sites not subjected to prolonged flooding and may grow where the water table is within 15 cm to 25 cm (6 to 10 in) of the surface. It is markedly less tolerant of such conditions than are red maple *(Acer rubrum)* and sweetgum *(Liquidambar styraciflua)*. Beech trees on poorly drained sites have shallower root systems than those on better drained sites *(39)*. Timber stands containing considerable numbers of beech are found on soils ranging from pH 4.1 to 6.0 *(39)*, but seldom where pH exceeds 7.0.

Beech is found at low elevations in the North and relatively high elevations in the southern Appalachians. Local soil and climatic factors probably determine whether beech grows at the higher elevations. In the Adirondacks of New York, low temperatures and wind keep beech below 980 m (3,200 ft), in contrast to the southern mountains where on the warmer slopes it grows at elevations up to 1830 m (6,000 ft). At latitudes in the middle of its range, however, beech is more abundant on the cooler and moister northern slopes than on the southern slopes *(39)*.

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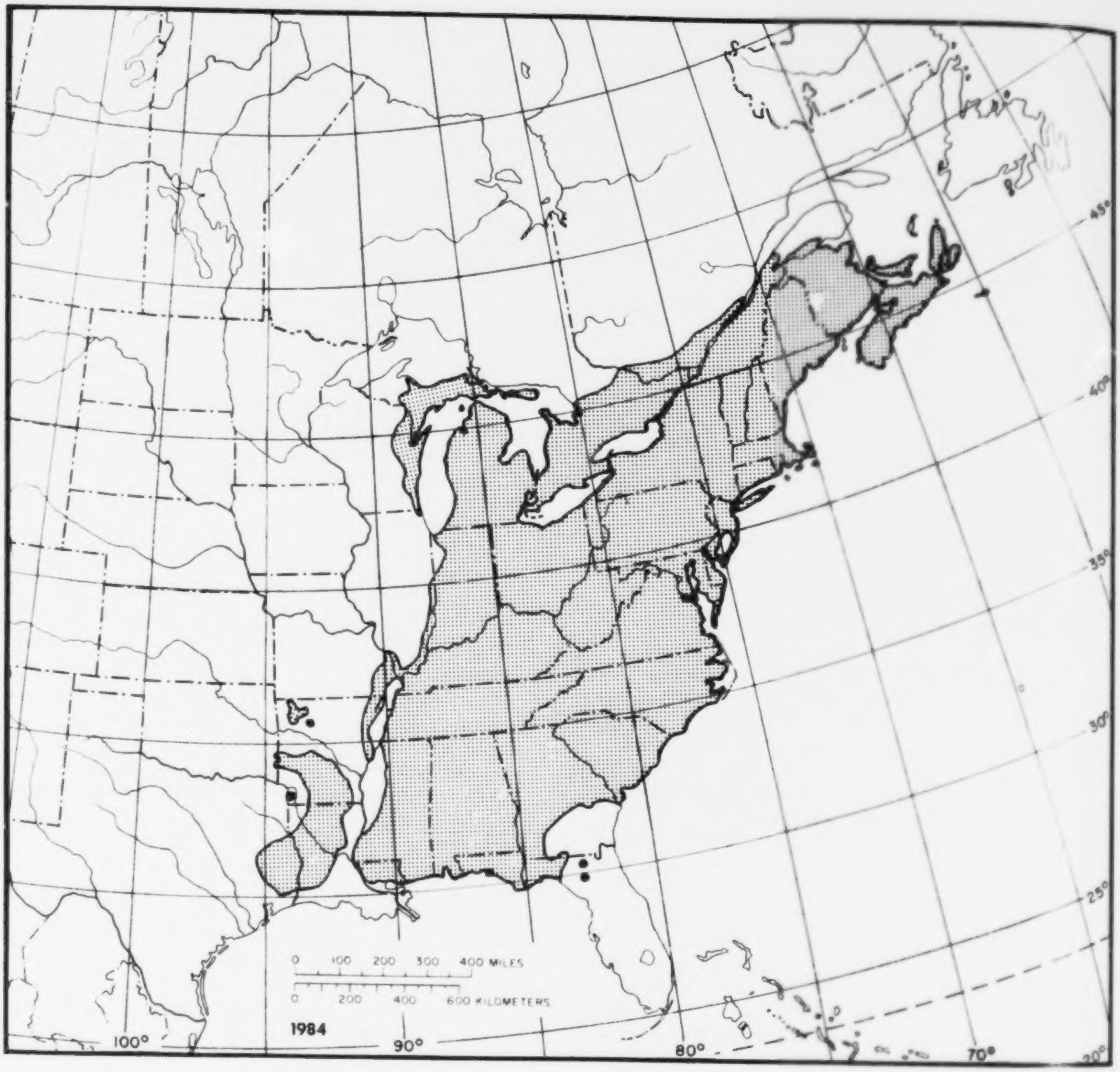

Figure 1—*The native range of American beech.*

Associated Forest Cover

Within its wide range in eastern North America, beech is associated with a large number of trees. Some of the principal associates are sugar maple, red maple, yellow birch *(Betula alleghaniensis)*, American basswood *(Tilia americana)*, black cherry *(Prunus serotina)*, southern magnolia *(Magnolia grandiflora)*, eastern white pine *(Pinus strobus)*, red spruce *(Picea rubra)*, and several hickories *(Carya* spp.) and oaks *(Quercus* spp.). Beech is included in 20 forest cover types and is a major component in the following three *(5)*: Sugar Maple-Beech-Yellow Birch (Society of American Foresters Type 25), Red Spruce-Sugar Maple-Beech (Type 31), and Beech-Sugar Maple (Type 60). Beech is a minor species in 17 other cover types.

Life History

Reproduction and Early Growth

Flowering and Fruiting—In the Northern and Central States, beech flowers appear in late April or early May when the leaves are about one-third grown; the species is monoecious. The flowers are quite vulnerable to spring frosts. Male flowers occur in long-stemmed heads; female flowers in clusters of two to four *(40)*. Beechnuts require one growing season to mature and they ripen between September and November. Two or (rarely) three nuts may be found within a single bur. The first nuts to fall are usually wormy or aborted.

Seed fall begins after the first heavy frosts have caused the burs to open and is completed within a few weeks. Some empty burs remain on the trees throughout the winter.

Seed Production and Dissemination—Beech ordinarily begins to produce a substantial amount of seeds when about 40 years old, and by the time it is 60 years old may produce large quantities. Good beech seed crops are produced at 2- to 8-year intervals *(40)*.

Beech seeds, averaging about 3,500/kg (1,600/lb), are relatively heavy. Most of the seeds simply drop to the ground under the parent trees. Rodents may carry some of them short distances and on steep terrain a few may roll down slopes, but dispersal is quite restricted. Bluejays may transport many beech seeds several kilometers *(16,17)*.

Seedling Development—Beech seeds germinate from early spring to early summer. Germination is epigeous and chilling is required to break dormancy. On either mineral soil or leaf litter, germination is good, but on excessively wet sites it is poor. Both germination and survival tend to be better on mor humus than on mull humus soil *(39,40)*.

Beech seedlings develop better under a moderate canopy or in protected small openings than they do on larger open areas where the surface soil may dry out below the depth of the shallow roots. Height growth of seedlings is about the same in dense (87 percent) or moderate (55 percent) shade, but total dry weight and root development are greatest under moderate shade. Height growth, dry weight, and root development in the open are less than in shade *(25)*. Seedlings are found in large numbers beneath even the densest stands, but under such conditions their growth is slow. Beech reproduction can start under, and come through, fern and raspberry cover.

Dormancy of beech seedlings can be broken in spring and growth can be prolonged in fall by supplemental light. Decreasing day length plays the major role in inducing dormancy in the fall, but day length may be secondary to temperature in controlling resumption of growth in the spring. That is, day length probably becomes adequate for growth to resume in the spring before temperatures are high enough for growth to occur. Temperature, therefore, exerts the final control over growth resumption.

Beech continues growing all winter in a greenhouse when daylight is supplemented by continuous artificial light.

The height of beech seedlings growing in the intense competition of a virgin hemlock–hardwood stand in northern Pennsylvania *(39)* was as follows:

Age	**Total height**	
yr	*m*	*ft*
6	0.3	1
10	0.6	2
14	0.9	3
17	1.2	4
18	1.4	4.5
20	1.5	5
22	1.8	6
25	2.1	7

When forest stands are heavily cut, beech reproduction tends to grow more slowly than that of most associated hardwood species. This is especially true in clearcuttings. Here the beech reproduction may be overtopped by less tolerant species, such as the birches and white ash (*Fraxinus americana*), that respond vigorously to increased light. A number of studies have shown that heavy cutting or clearcutting results in fewer beech in the new stand than in the old *(39)*. Repeated clearcutting on short rotations may nearly eliminate beech. Under partial cuttings, especially single-tree selection cuttings, intolerant species offer little competition and the tolerant beech reproduction is able to develop. The beech may be further favored by its virtual immunity to deer browsing.

Vegetative Reproduction—Beech sprouts well from the stumps of young trees, but this ability diminishes after trees reach 10 cm (4 in) in d.b.h. Sprouts from stumps 25 cm to 38 cm (10 to 15 in) in diameter usually are short lived and do not attain tree stature. Numerous sprouts may develop on the trunk of beech immediately below a wound, and from the tops of stumps; here adventitious buds develop in callus tissue of the cambial region.

Beech trees may develop large numbers of root sprouts or suckers. Studies *(30)* have shown that reproduction is almost exclusively by suckering in the "beech gaps" and is abundant in the Adirondack Mountains of New York, in Maine *(13)*, and in many other areas, often those near the northern and western limits of its range *(11,42)* where environments are severe *(27)*. Suckering is stimulated only slightly by removal of the stem *(18)*. Injury to roots appears to be necessary for the initiation of root sprouts in beech *(19)*. Root sprouts arise from adventitious buds that form within callus tissues associated with wounds. Experimental injuries to roots in November resulted in fewer sprouts than did injuries inflicted in spring *(20)*. Sometimes root sprouts develop where no apparent injury has occurred *(39)*. There were relatively more root sprouts on southerly slopes in areas where freeze–thaw action tended to injure shallow or exposed roots and stimulate sprout formation, and where late spring frosts tended to injure or kill young seedlings. In Ohio, seedling regeneration was positively associated with northerly exposures and root sprout regeneration with southerly exposures *(11)*.

In an undisturbed stand of mature beech in the Adirondacks, 1,730 to 2,220 root sprouts per hectare (700 to 900/acre; 7 to 12/tree) were counted *(39)*. Casual observations elsewhere indicate that the number per tree may greatly exceed this figure.

Root sprouts can develop into desirable trees. Isozyme genetic studies have shown that some groups of overstory beech trees with similar phenotypic traits are clones *(14)*. Sometimes root sprouts are ephemeral. In one reproduction study, made after a 60-year-old stand of beech was cut, all of the root sprouts died within 4 years. On the other hand, the trees in a 40-year-old beech stand of sprout origin averaged 10 cm (4 in) in d.b.h. and 11.6 m (38 ft) in height.

Beech limbs root in a single year when layered. Interspecific root grafting is common.

Sapling and Pole Stages to Maturity

Growth and Yield—Beech's period of radial growth may continue for 80 to 89 days in the Georgia Piedmont and for approximately 60 days in Indiana *(39)*. Annual height growth of beech saplings is complete in about 60 days; 90 percent of this growth occurs between May 10 and June 10. American beech has a lower site index than any associated hardwood in the northern Lake States.

The radial growth period is influenced by available soil moisture. Under normal conditions, it may end in the middle of July, but drought may end it in mid-June. A few individual trees may continue their growth into August and September. In dry years, annual rings may not grow in the basal sections of some beech trees. In general, radial growth of beech begins when the leaves are fully expanded.

Table 1—Characteristics of American beech growing in the Lake States

Age	D.b.h.	Height	Volume
yr	*cm*	*m*	*m³*
20	2	4.0	—
40	6	8.5	—
60	10	11.9	0.03
80	14	14.6	0.10
100	18	17.4	0.22
150	29	22.9	0.76
200	40	25.6	1.58
250	51	26.8	2.69
yr	*in*	*ft*	*ft³*
20	0.7	13	—
40	2.3	28	—
60	3.8	39	1.0
80	5.4	48	3.7
100	7.1	57	7.9
150	11.5	75	27.0
200	15.7	84	56.0
250	19.9	88	95.0

The annual diameter increment of beech of pole and small saw-log size averages from around 1.8 to 2.3 mm (0.07 to 0.09 in) in undisturbed second-growth stands to 3.8 to 4.8 mm (0.15 to 0.19 in) in trees released by partial cuttings *(35,39)*. Annual growth of poles for 5 years after heavy release, leaving from 1.1 to 4.6 m²/ha (5 to 20 ft²/acre) of basal area, ranged from 5.6 mm (0.22 in) to 7.6 mm (0.30 in); growth was better in the most heavily stocked stands and on trees with good crown development *(26)*.

Under optimum conditions, beech trees may become 37 m (120 ft) high; however, they generally average 18 to 24 m (60 to 80 ft). Growth data for beech in the Lake States are shown in table 1.

Among 12 broad-leaved species rated according to their longevity, beech was exceeded only by white oak and sugar maple. Beech trees older than 366 years have been found in Pennsylvania. The distribution of numbers of trees by age is "J" shaped, typical of tolerant long-lived species *(21)*. One of the largest beeches on record, growing in Michigan, is 135 cm (53.2 in) in d.b.h., 49 m (161 ft) tall, and has a crown 32 m (105 ft) wide.

Beech trees prune themselves in well-stocked stands. Open-grown trees, however, develop short, thick trunks with large, low, spreading limbs terminating in slender, somewhat drooping branches that form a broad, round-topped head.

Beech trees that have been injured or suddenly exposed by stand cuttings often develop epicormic branches. In one stand where 65 percent of the basal area had been cut, 40 percent of the remaining beech trees had epicormic branches 5 years later, whereas in a similar but uncut stand, only 17 percent of the trees had such branches *(39)*. Epicormic branching of beech trees has also been observed after glaze damage and after low-temperature injury *(27)*. One report on winter injury showed epicormic branches to be restricted largely to trees with d.b.h. of 10 cm (4 in) or less *(2)*.

Rooting Habit—Young seedlings have a taproot that gives way to a heart root system as the tree matures *(41)*. The root system is generally shallow but may penetrate to 1.5 m (5 ft) or more in deep soils. The fine roots form a dense mat in our soil types. Beech root systems are more shallow than the associated yellow birch and sugar maple. Few tree species are less tolerant of flooding during the growing season than American beech.

Root exudates of beech contain more organic acids than those of sugar maple or yellow birch.

Reaction to Competition—Beech is classed as very tolerant of shade. In some parts of its range, beech is the most tolerant species. Its tolerance is partly due to its very low respiration rate *(24)* and the quick response of the stomata, which open when light suddenly increases and rapidly close when light intensity diminishes. Beech stomata are more responsive than those of red maple, red oak *(Quercus rubra)*, or yellow-poplar *(Liriodendron tulipifera)*, which are less tolerant *(43)*. On very poor soils or in very cold climates, beech may be less tolerant. The tolerances of beech and associated sugar maple are about the same *(25)*, although locally one species or the other may predominate in the forest understory. Factors other than the ability to endure shade appear to govern the relative success of beech and its common tolerant competition, sugar maple, eastern hemlock *(Tsuga canadensis)*, and balsam fir *(Abies balsamea)*. Beech may be more competitive under somewhat adverse site and climate conditions *(39)*.

Beech and sugar maple are recognized as climatic climax species in the northern hardwood types of the Northeast, Lake States, and Appalachian Mountains. In the Southeast, relict areas of beech suggest that an original maple-beech association has been displaced by the once subclimax oak-hickory community.

Damaging Agents—In regions with low winter temperatures, long frost cracks often appear in the tree trunks. These cracks are sometimes superficial but sometimes extend deep into the bole. In the Northeast, beech has been damaged or killed by temperatures of -40° to -45° C (-40° to -50° F) preceded by severe droughts *(39)*. Injured trees died the following summer and winter. Beech can be severely damaged by late spring frosts.

In a Kentucky study of effects of flooding, beech was one of the more sensitive species. Beech trees were killed by 2 weeks of submergence of their root crowns in summer. An 18-day period of flooding in winter had no apparent adverse effect, however.

Beech's susceptibility to glaze-storm breakage is no greater than that of its associated hardwoods and may be somewhat less than the average for a mixed stand *(39)*. Except on shallow soils, beech is rather windfirm.

The thin bark of beech renders it highly vulnerable to injury by fire (large shallow roots are especially vulnerable), sunscald, logging, pruning, or disease. When large branches are broken they heal comparatively slowly *(38)* and serve as entrance courts for a host of decay fungi *(12,32)*.

More than 70 decay fungi (a record for a hardwood species) have been reported for beech *(12)*. The most important include *Daedalea unicolor, Ganoderma applanatum, Fomes fomentarius, Phellinus igniarius, Hericium erinaceus, H. coralloides, Steccherinum septentrionale, Inonotus glomeratus,* and *Ustilina vulgaris*. The shoestring fungus, *Armillaria* sp., the most important root pathogen, attacks and girdles roots of weakened trees. Beech roots are also parasitized by the broomrapes, *Conopholis americana* and *Epifagus virginiana*. The latter, beech drops, is specific to beech *(8,34)*.

The thinness of beech bark also makes it vulnerable to an unusually large number of sucking insects, including the beech blight aphid, *Fagiphagus imbricator*, and the giant bark aphid, *Longistigma caryae*. Continuous heavy outbreaks of the oystershell scale, *Lepidosaphes ulmi*, have resulted in severe crown dieback and even in the death of entire stands *(1)*. *Xylococculus betulae*, another scale, causes roughened spots on stems of young trees and is especially devastating to the sprout thickets that have emerged in the aftermath of beech bark disease (fig. 2), the most serious problem of this species *(13,31)*.

Beech bark disease is initiated when yet another scale insect, the beech scale, *Cryptococcus fagisuga*, attacks the bark of beech trees and renders it susceptible to bark canker fungi of the genus *Nectria* *(3,33)*. The insect component of this scale-*Nectria*

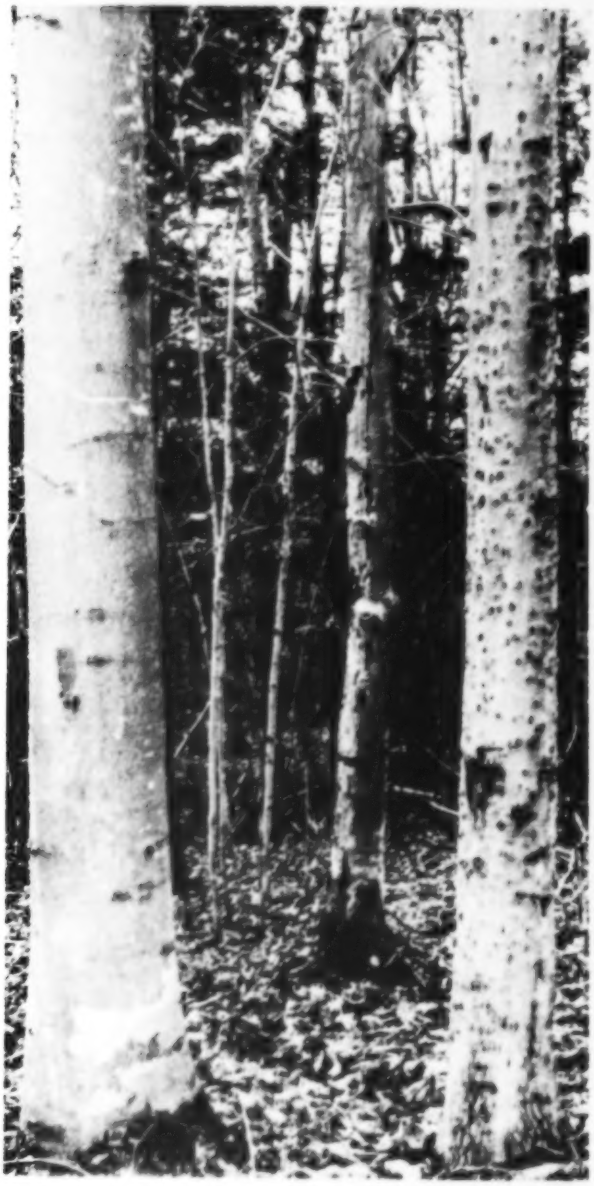

Figure 2—The American beech tree on the left is free of the beech bark disease; the two trees on the right are infected severely.

"complex" was introduced to Nova Scotia from Europe around 1890 and is now found throughout New England, New York *(15)* and northern Pennsylvania *(37)*. In 1981, a 70,000-acre infestation was detected in northeastern West Virgina, many miles south of the nearest previously known infestation *(28)*. More recently, the disease has been reported as far west as Toronto, Ontario, and the scale is now present in northeastern Ohio and northwestern Virignia *(29)*. In North America, *Nectria coccinea* var. *faginata* is the fungus most commonly associated with the disease in the Maritime Provinces, New England, and northern New York. In western Pennsylvania, West Virginia, and some New York stands however, *N. galligena* is the predominant associated species. As the disease and forest interact for the first time, mortality may be so severe that a large proportion of the big, mature beech trees are killed. Mortality is now especially high in some southern and western areas of the Adirondack Mountain region. The percent stocking of beech was reported *(7)* to remain the same after the killing front of the beech bark disease moved through a managed stand; the disease mainly affected the larger trees. Although such mortality is rare in stands emerging in the aftermath of the disease, severe defect may be caused by the now-endemic causal complex together with *Xylococculus betulae (13)*.

Defoliation by insects can occasionally be a serious problem *(1)*. The most damaging is the saddled prominent, *Heterocampa guttivitta*, although the forest tent caterpillar *(Malacosoma disstria)*, gypsy moth *(Lymantria dispar)*, fall cankerworm *(Alsophila pometaria)*, and the Bruce spanworm *(Operophtera bruceata)* occasionally cause heavy defoliation in local areas. Insect defoliation often renders trees susceptible to attack by the shoestring root fungus.

Beech is seldom severely browsed by white-tailed deer. When other, more desirable tree species are available, beech is usually nipped only sparingly *(36)*.

Special Uses

Beech mast is palatable to a large variety of birds and mammals, including mice, squirrels, chipmunks, black bear, deer, foxes, ruffed grouse, ducks, and bluejays. Beech is the only nut producer in the northern hardwood type. Beech wood is used for flooring, furniture, turned products and novelties, veneer, plywood, railroad ties, baskets, pulp, charcoal, and rough lumber. It is especially favored for fuelwood because of its high density and good burning qualities.

Creosote made from beech wood is used internally and externally as a medicine for various human and animal disorders. (It is important to note that coal tar creosote, the kind used to protect wood from rots, is highly toxic to humans.)

Genetics

Fagus grandifolia Ehrh. is the only type species of American beech now recognized in North America *(9,10,23)*. Some botanical authorities hold that Northern and Southern beeches vary, and have described the southern form as *F. grandifolia* var. *caroliniana* (Loud.) Fern. & Rehd., Carolina beech *(4,6)*. A previously named species in the mountains of Mexico *(39)* has been renamed a variety, *F. grandifolia* var. *mexicana* (Martinez) Little *(22)*.

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Fraxinus americana L. White Ash

Oleaceae Olive family

Richard C. Schlesinger

White ash *(Fraxinus americana)*, also called Biltmore ash or Biltmore white ash, is the most common and useful native ash but is never a dominant species in the forest. It grows best on rich, moist, well-drained soils to medium size. Because white ash wood is tough, strong, and highly resistant to shock, it is particularly sought for handles, oars, and baseball bats. The winged seeds provide food for many kinds of birds.

Habitat

Native Range

White ash (figs. 1, 2) grows naturally from Cape Breton Island, Nova Scotia, to northern Florida in the east, and to eastern Minnesota south to eastern Texas at the western edge of its range *(7)*.

Climate

The climate varies greatly within the natural range of this species. The length of the frost-free period is from 90 to 270 days. Mean January temperatures range from -14° C (7° F) to 12° C (54° F) and the mean annual minimum temperatures range from -34° C (-30° F) to -5° C (23° F). Mean July temperatures range from 18° C (64° F) to 27° C (81° F). The average annual precipitation is between 760 and 1520 mm (30 and 60 in), and the snowfall is from 0 to 250 cm (100 in).

Soils and Topography

White ash has demanding soil fertility and soil moisture requirements. These requirements may be provided by soils derived from a variety of parent materials—limestone, basalt, shale, alluvium, and fine glacial till. A large number of soil types may support white ash, many of which are included in the Hapludalfs and Fragiudalfs of the order Alfisols, Haplorthods and Fragiorthods of the order Spodosols, and Dystrochrepts and Fragiochrepts of the order Inceptisols *(11)*.

White ash grows most commonly on fertile soils with a high nitrogen content and a moderate to high calcium content. Nutrient culture results show that an absence of nitrogen reduces seedling dry weight by 38 percent compared to seedlings grown in complete nutrient solution, and that calcium is the second most important macroelement, followed by sulfur *(3)*. Its pH tolerance varies from 5.0 to 7.5.

Soil moisture is an important factor affecting local distribution. Best growth occurs on moderately well drained soils, including areas underlain by compacted glacial till; light textured, well drained, glacial drift; and sandy to clay loam soils in which roots can penetrate to a depth of 40 cm (16 in) or more. Although rarely found in swamps, white ash is intermediately tolerant of temporary flooding.

White ash is found in various topographic situations. It grows from near sea level in the southeastern Coastal Plain to about 1050 m (3,450 ft) in the Cumberland Mountains and up to 600 m (1,970 ft) in New York's Adirondack Mountains. In the hilly and mountainous areas of the Northeast, it grows on the mesophytic lower and middle slopes, usually stopping short of both the dry, oak–pine ridgetops and the cold, spruce–fir mountain tops. In the Coastal Plain, white ash usually is limited to the slightly elevated ridges in the floodplains of major streams. In the Central States it is most common on slopes along major streams, less common in upland situations, and rarely found in the flat bottoms of major streams or in depressions *(16)*.

Associated Forest Cover

White ash is a major component in the forest cover type White Pine–Northern Red Oak–Red Maple (Society of American Foresters Type 20) and is a common associate in 25 other forest cover types *(4)*:

19	Gray Birch–Red Maple
21	Eastern White Pine
22	White Pine–Hemlock
23	Eastern Hemlock
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
26	Sugar Maple–Basswood
27	Sugar Maple
28	Black Cherry–Maple
33	Red Spruce–Balsam Fir
39	Black Ash–American Elm–Red Maple
42	Bur Oak
52	White Oak–Black Oak–Northern Red Oak
53	White Oak
55	Northern Red Oak
57	Yellow-Poplar

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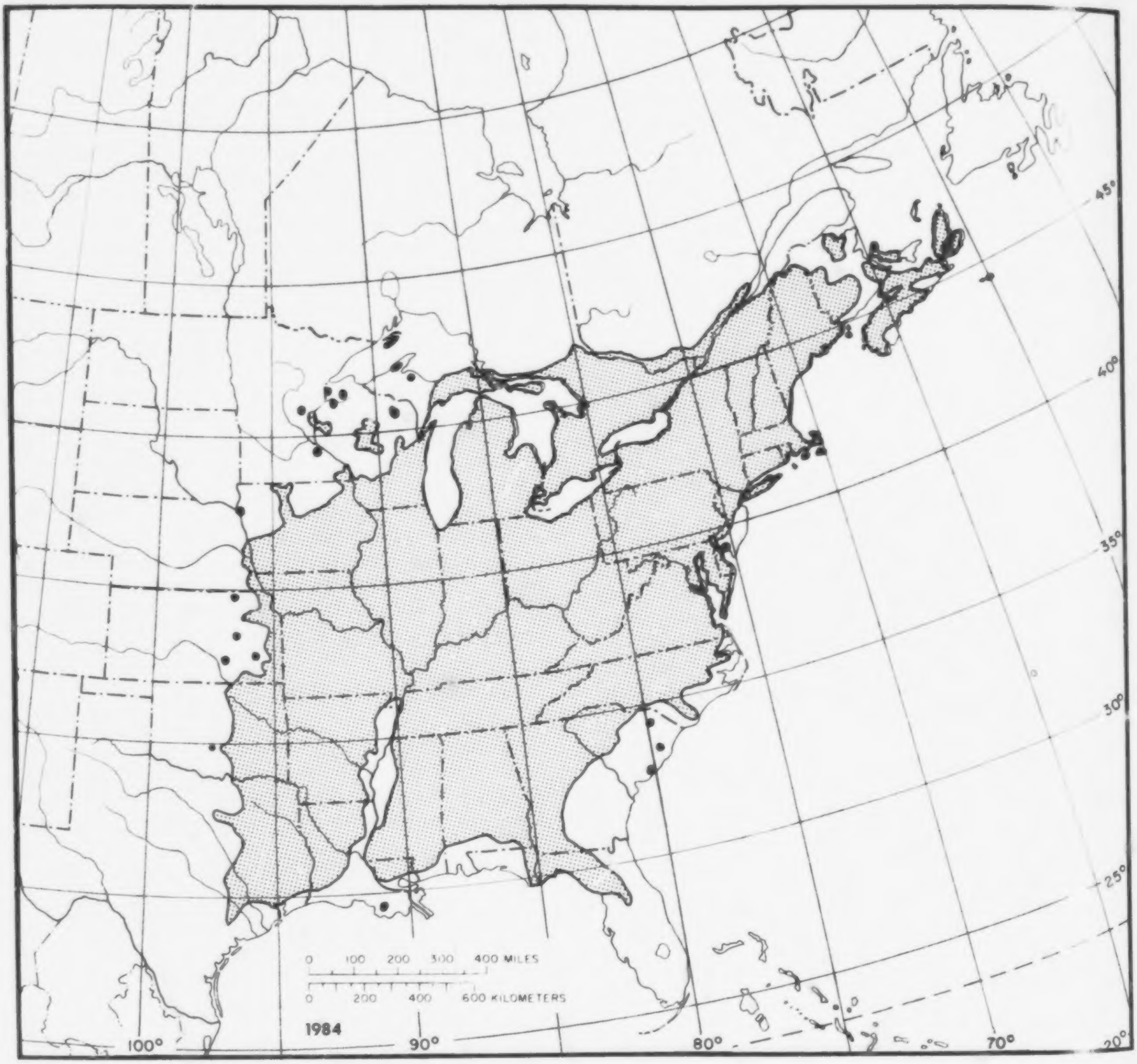
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Figure 1—*The native range of white ash.*

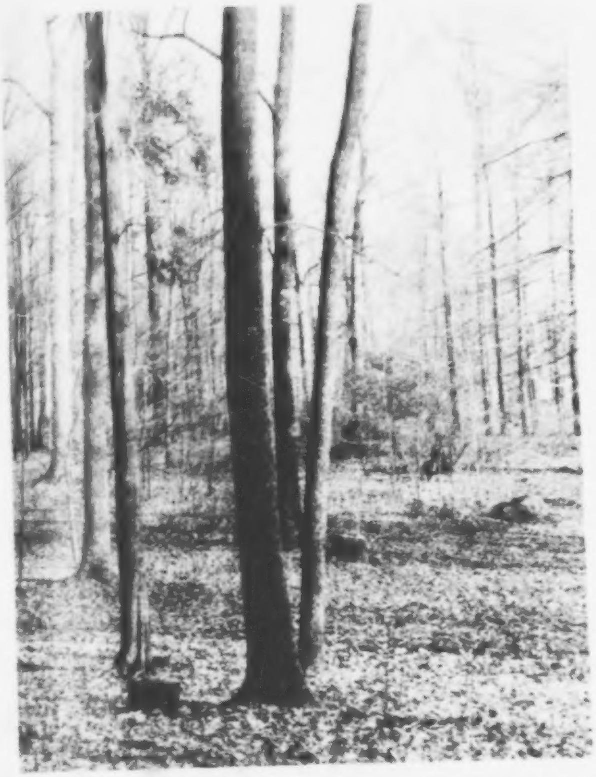

Figure 2—*A 60-year-old white ash 36 cm (14 in) in d.b.h.*

58	Yellow-Poplar–Eastern Hemlock
59	Yellow-Poplar–White Oak–Northern Red Oak
60	Beech–Sugar Maple
63	Cottonwood
64	Sassafras–Persimmon
80	Loblolly Pine–Shortleaf Pine
82	Loblolly Pine–Hardwood
87	Sweetgum–Yellow-Poplar
91	Swamp Chestnut Oak–Cherrybark Oak

Some of the primary associates of white ash include eastern white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), American basswood (*Tilia americana*), eastern hemlock (*Tsuga canadensis*), American elm (*Ulmus americana*), and yellow-poplar (*Liriodendron tulipifera*). Understory shrubs and small trees frequently found growing with ash are downy serviceberry (*Amelanchier arborea*), pawpaw (*Asimina triloba*), American hornbeam (*Carpinus caroliniana*), flowering dogwood (*Cornus florida*), witch-hazel (*Hamamelis virginiana*), eastern hophornbeam (*Ostrya virginiana*), and mapleleaf viburnum (*Viburnum acerifolium*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—White ash is dioecious; flowers appear with or just before the leaves in April and May. A good seed crop is produced about every third year. The time between the first noticeable enlargement of the male flower buds until shedding is 2 to 3 weeks. Pollen shedding from an individual tree usually takes 3 or 4 days. The pollen is carried by wind as far as 100 m (328 ft) from the point of dispersion.

Female buds are completely open a few days after they begin to swell. Exposed flowers remain receptive for about 1 week, but once the stigmas discolor, the period of receptivity is past. Abundant seed crops are borne by about half of the flowering trees.

Good seeds are produced in all parts of the crown. Almost 99 percent of the fruits (samaras) contain one seed, about 1 percent contain two, and a very small percent have twin embryos. Vigorous trees may first flower when only 8 to 10 cm (3 to 4 in) in d.b.h., but white ash is usually 20 to 25 cm (8 to 10 in) in d.b.h. before it flowers abundantly.

Seed Production and Dissemination—The seed is dispersed by wind up to 140 m (460 ft) from the parent tree. White ash seed has a very pronounced dormancy. Although the embryo is completely developed morphologically at the time of seedfall (September to December), the physiological state of the endosperm and embryo inhibit germination. Seeds must be stratified under moist conditions for 2 or 3 months before they will germinate, and the average laboratory germination is 54 percent. The minimum seed-bearing age is 20 years (*14*).

Seedling Development—Germination is epigeal. Natural regeneration from seeds will occur if the soil, humus, or leaf litter is wet in the spring. Under experimental conditions, seedlings developed best in 45 percent of full sunlight (*8*). Thus silvicultural systems that can provide sunlight, such as shelterwood or clearcutting, have been recommended for white ash.

Photoperiodic response appears to vary with geographic location. North Carolina seedlings showed no growth response to a 14.5-hour daylength. In a Massachusetts test, however, northern seedlings ceased height growth and dropped their leaves well before the first frost, while southern seedlings continued height growth until late autumn.

Vegetative buds begin to enlarge in April or May. Height growth is 90 percent complete in 30 days, and 100 percent complete in 60 days. Diameter growth generally continues until August.

Young white ash exhibits strong apical dominance. Thrifty open-grown seedlings 2 m (6.6 ft) tall often have only two or three pairs of lateral branches, and sometimes none. If the terminal bud is removed, apical dominance is altered and new branches develop from the uppermost pair of lateral buds. Generally one of these grows faster than the other and soon assumes apical control.

Vegetative Reproduction—Stumps of freshly cut seedling and sapling white ash sprout readily. Usually only one or two stems are produced. This species can be propagated by conventional methods of budding, grafting, or layering. Even open field and bench grafting or unpotted stock are highly successful. Diploid, tetraploid, and hexaploid white ash have all been successfully grafted on diploid stock.

Sapling and Pole Stages to Maturity

Growth and Yield—Depending on the amount of root competition, a field-grown white ash tree in full sunlight may take from 3 to 15 years to become 1.5 m (5 ft) tall. By then, its root system is usually well established and white ash is able to grow rapidly even if surrounded by weeds. Post-juvenile growth rates of dominant and codominant trees in unthinned, even-aged stands in central Massachusetts are as follows:

Age	D.b.h.		Height	
yr	*cm*	*in*	*m*	*ft*
20	10	4	12	39
30	18	7	17	56
40	25	10	21	69
50	30	12	23	75
60	36	14	25	82
70	43	17	27	89

Yield tables are not available for white ash in pure stands. However, for plantations in Canada ranging in age from 20 to 38 years, the growth of the dominant and codominant trees averaged 3 to 5 mm (0.1 to 0.2 in) per year in diameter and 0.2 to 0.8 m (0.7 to 2.6 ft) in height *(13)*. In mixed Appalachian hardwood stands, diameter growth ranged from 3 to 8 mm (0.1 to 0.3 in) per year, depending on site quality and individual tree variation.

Rooting Habit—White ash generally forms a taproot that in turn branches into a few large roots that grow downward. From these vertical roots, single lateral branches develop at intervals. Intraspecific grafting is common. The distribution of roots is strongly influenced by soil type. On a loamy sand, most of the roots, both large and small, were in the A horizon. On a fine sandy loam, the majority of the fine roots were in the B_1 horizon, and the large roots equally in the A and B_1.

Knowledge of mycorrhizal associations is limited. *Gyrodon merulioides* has been reported on white ash. Seedlings inoculated with the endomycorrhizal fungi *Glomus mosseae* and *G. fasciculatus* grew markedly better than nonmycorrhizal controls *(12)*.

Reaction to Competition—White ash is a pioneer species that establishes itself on fertile abandoned fields in several parts of the country. In the Southeast, much of the abandoned agricultural land is incapable of supporting white ash. On such sites, white ash establishes itself only after some site protection and improvement has been accomplished by pines. However, pioneer ash often do not develop into good timber trees unless other hardwoods or pines are also present to provide competition and reduce branchiness.

Open-grown trees commonly remain single stemmed and fine branched until they are 9 to 12 m (30 to 40 ft) tall, although old specimens can become as broad crowned as an elm. With even slight crowding, the single-stemmed characteristic can easily be maintained throughout a rotation. Shade-killed branches drop quickly—small ones within a year or two and larger ones within 4 or 5 years *(16)*.

Uninjured terminal buds suppress the growth of all lateral buds on the current year's growth, and they suppress the growth of other laterals to such an extent that each internode has only one pair of branches that persist more than a few years. Even the strongest lateral branches grow only half as fast as the terminal except on old, open-grown trees. Little or no epicormic branching occurs on the boles of released trees. The branches of dominant trees emerge from the bole at about a 35° angle from the vertical, whereas the branches of intermediate trees emerge at about a 55° angle *(16)*.

When young, white ash is a shade-tolerant tree. Seedlings can survive under a canopy with less than 3 percent of full sunlight but grow little under these conditions. Seedlings that receive sufficient sunlight grow rapidly. With increasing age, white ash becomes less tolerant of shade and is classed overall as intolerant. The decrease in shade tolerance with increasing age is reflected in the fact that young white ash is abundant in the understory of northern hardwood stands, but few grow into the overstory unless provided with light from above.

Despite its low shade tolerance, white ash is characteristic of intermediate as well as early stages of natural plant succession. Throughout its range it is a minor but constant component of both the understory and overstory of mature forests on suitable soils. It owes its position in the final overstory to its ability to persist for a few years in moderately dense shade and to respond quickly to openings in the canopy created by death or other causes.

White ash can be maintained more easily in a dense stand than can some of its more shade-intolerant associates, such as northern red oak. In contrast, dominant or codominant white ash responds readily to thinning and within a few years will increase its crown area to take full advantage of any reasonable release *(16)*.

Damaging Agents—Ash decline (also called ash dieback) is the most serious problem affecting white ash. Especially prevalent in the northeastern part of the tree's range, this disease complex occurs from the Great Plains to the Atlantic coast between 39 and 45 degrees north latitude *(10)*. The disease, ash yellows, caused by mycoplasma-like organisms (MLO), has been found associated with most of the dying trees where ash decline is conspicuous *(9)*. However, since not all dying trees are infected with MLO, ash decline is thought to result from multiple causes. Drought-weakened trees may be invaded by canker-causing, branch-girdling fungi such as *Fusicoccum* spp. and *Cytophoma pruinosa*. Additional stresses that may be involved in the etiology of ash decline are air pollution, leaf-spotting fungi, and viruses. Control recommendations are based primarily on maintaining good tree vigor *(6)*.

Air pollution damages white ash. It is rated as sensitive to ozone and is severely injured by stack gases from soft coal consumption and from industrial processes, both of which emit sulfur dioxide.

Two leaf spot fungi, *Mycosphaerella effigurata* and *M. fraxinicola*, are common in nurseries and in the forest and cause premature defoliation of white ash. Anthracnose *(Gloeosporium aridum)* also causes premature defoliation and is most serious following exceptionally wet springs. An ash strain of tobacco ringspot virus causes chlorotic areas on the leaves and has been associated with ash dieback.

A rust *(Puccinia peridermiospora)* distorts petioles and small twigs. Cankers caused by *Nectria galligena* may cause branches to break but are rarely found on main stems. Heartwood rots may be caused by *Perenniporia fraxinophilus*, *Phellinus igniarius*, *Pleurotus ostreatus*, *Tyromyces spraguei*, and *Laetiporus sulphureus*. These organisms usually enter through wounds or broken branches, mainly on older trees.

Of 26 species of nematodes reported from the roots or root zones of white ash, only one, *Meloidogyne ovalis*, has been associated with root injury. However, nematodes can be vectors for the ringspot virus *(5)*.

Of the insect pests, the oystershell scale *(Lepidosaphes ulmi)* is the most serious. Severe infestations cause yellowing of the leaves, and if prolonged, may kill some trees. The cottony maple scale *(Pulvinaria innumerabilis)* also attacks white ash.

The brownheaded ash sawfly *(Tomostethus multicinctus)* and the blackheaded ash sawfly *(Tethida cordigera)* are defoliators that are of concern mainly on ornamental trees. The forest tent caterpillar *(Malacosoma disstria)* and the green fruitworm *(Lithophane antennata)* feed on forest trees and occasionally cause complete defoliation within small geographic areas. The larvae of sphingid moths—*Sphinx chersis* (the great ash sphinx), *S. kalmiae*, and *Ceratomia undulosa*—feed on the leaves of white ash, as does the notched-wing geometer *(Ennomos magnaria)*. The larvae of two leaf roller moths, *Sparganothis dilutocostana* and *S. folgidipenna*, also feed on ash.

The ash bark beetle *(Leperisinus aculeatus)* may cause slight injury when the adults bore into the bark to hibernate. The ash borer *(Podosesia syringae)* may seriously damage young shade and shelterbelt trees. The ash and privet borer *(Tylonotus bimaculatus)* attacks and kills branches, especially on older trees. Both the red-headed ash borer *(Neoclytus acuminatus)* and the banded ash borer *(N. caprea)* colonize cut logs and dead or dying trees *(1)*.

White ash seedlings are easily damaged or destroyed by deer and cattle browsing. Rabbits, beaver, and porcupine occasionally use the bark of young trees for food.

Special Uses

One of the earliest reported uses of white ash was as a snake bite preventive. Ash leaves in a hunter's pocket or boots were "proved" to be offensive to rattlesnakes and thereby provided protection from them. Seeds of white ash are eaten by the wood duck, bob white, purple finch, pine grosbeak, and fox squirrel. White ash is used in yard, street, and roadside plantings and also has been planted on strip mines with some success.

Genetics

Population Differences

White ash contains several phenotypic variants of leaf form that appear to be genetically controlled even though they are randomly distributed throughout the natural range. Chief among these are 9-leaflet, narrow-leaflet, blunt-leaflet, ascidiate leaflet, partially pubescent, purple-keyed, and crinkle-leaf forms. A purple leaf variant is vegetatively propagated and grown as an ornamental.

White ash is a polyploid species. Diploids (2n=46) occur throughout the species range but most tetraploids (2n=92) are found south of latitude 35° N and hexaploids (2n=138) are concentrated between latitude 35° and 40° N. Although three ecotypes were previously recognized on the basis of seedling morphology and ploidy level *(15)*, recent work has shown that the variation in several traits is closely related to latitude. This clonal variation and the strong effects of ploidy level on several other traits indicate that ecotypes probably do not exist in white ash *(2)*.

Hybrids

White ash and Texas ash *(Fraxinus texensis* (Gray) Sarg.) intergrade in Texas. The pumpkin ash *(Fraxinus profunda* (Bush) Bush) behaves in many respects as if it were a true breeding hexaploid derivative of a cross between tetraploid white ash and diploid green ash *(Fraxinus pennsylvanica* Marsh.). However, attempts have failed to artificially cross the two species. It is likely that natural hybridization between white ash and other species is extremely rare *(16)*.

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Fraxinus latifolia Benth. Oregon Ash

Oleaceae Olive family

Peyton W. Owston

Oregon ash *(Fraxinus latifolia)* is the only native species of *Fraxinus* in the Pacific Northwest. It is commonly found in riparian habitats and is not managed for timber production. This tree may reach the age of 250 years and is fast growing the first third of those years, then grows slowly. The seeds are eaten by birds and squirrels. The wood is most used as fuelwood.

Habitat

Native Range

Oregon ash (fig. 1) is found from northern Washington to southern California. Some trees found growing wild in southwestern British Columbia are thought to have come from seed disseminated by planted ornamentals *(14)*. In Washington, Oregon ash grows along the shores of Puget Sound, in the western Cascade Range, and along the southwestern coast, but not in the Olympic Mountains *(22)*. It grows along the Columbia River from the coast east to The Dalles in Oregon *(22)*. In western Oregon, it occurs from the coast into the western Cascades and is prominent in the valleys—particularly the Willamette Valley *(2)*. More than 2.5 million m^3 (90 million ft^3) of growing stock occur in Oregon and Washington *(12)*. In California, Oregon ash is found in the north Coast Ranges as far south as Santa Clara County *(10)*. It also grows in the Sierra Nevada and in the delta region of the Great Valley. The species is prevalent in the canyons of the Pit and Sacramento Rivers *(7)*.

Climate

In the northern part of its range, Oregon ash grows where summers are generally cool and humid and winters are usually mild *(22)*. Mean annual temperatures are 8° to 9° C (46° to 48° F), and temperatures are usually not extreme. Precipitation ranges from 1500 to 3000 mm (59 to 118 in) annually and is generally well distributed from fall through spring. July and August are often rainless. In the valleys of western Oregon, mean annual temperatures are 11° to 12° C (52° to 54° F), and annual precipitation averages 510 to 1020 mm (20 to 40 in) *(3)*. In the southern part of its range, Oregon ash grows where summer temperatures are high and precipitation is low; humidity varies from high to low, depending on proximity to the Pacific Ocean *(22)*.

Soils and Topography

Although Oregon ash is sometimes found growing as high as 1520 m (5,000 ft) in elevation, it usually does not occur higher than 910 m (3,000 ft) *(6)*. Its preferred habitat is poorly drained, moist bottom land with deep soil rich in humus (fig. 2). In the central Willamette Valley of western Oregon, it is most commonly found on sites with silty clay loams and clays *(4)*. The species also grows in sandy soils or moist, rocky, gravelly soils *(2,22)*. It often follows streams and swamps in ribbonlike fringes *(2)* and is characteristic in seasonally flooded habitats *(3)*. Oregon ash is also found on adjacent forest sites at higher elevations, in old fields, and along roads *(2)*. It grows on Alfisols, Inceptisols, Mollisols, and Ultisols.

Associated Forest Cover

In the northern part of its range, Oregon ash is occasionally found in small pure stands, but it is usually associated with other trees, such as red alder *(Alnus rubra)*, bigleaf maple *(Acer macrophyllum)*, black cottonwood *(Populus trichocarpa)*, Oregon white oak *(Quercus garryana)*, and various willows *(Salix* spp.) *(2,3,8,22)*. In its drier habitats, it also grows with Douglas-fir *(Pseudotsuga menziesii)* and grand fir *(Abies grandis)* *(2,6,22)*. Associated species in southwestern Oregon and northern California are California-laurel *(Umbellularia californica)*, white alder *(Alnus rhombifolia)*, California sycamore *(Platanus racemosa)*, California black oak *(Quercus kelloggii)*, Oregon white oak, and ponderosa *(Pinus ponderosa)* and Digger pines *(P. sabiniana)* *(8,22)*. Oregon ash is an associate in the following forest cover types, Red Alder (Society of American Foresters Type 221), Black Cottonwood–Willow (Type 222), Port Orford-Cedar (Type 231), and Oregon White Oak (Type 233).

Understories in the riparian communities of western Oregon valleys vary from almost nothing under dense stands or in areas with recent silt deposits to herbaceous—typically sedges—or dense shrubby types *(3,4)*.

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Life History

Reproduction and Early Growth

Flowering and Fruiting—Oregon ash is dioecious; its small greenish flowers appear in dense, glabrous panicles with the leaves in April or May *(8,25)*. The fruits, oblong to elliptical samaras, ripen in August or September. They are 3 to 5 cm (1.25 to 2 in) long and 3 to 9 mm (0.1 to 0.33 in) wide, including the wing, and are light brown when mature *(10,18)*.

Seed Production and Dissemination—Seeds are produced about the 30th year *(2)*. Oregon ash is an abundant annual seeder in open stands or as isolated trees *(22)*, but heavy crops occur at 3- to 5-year intervals in forest stands *(2)*. Seeds are dispersed by wind in September or October. There are usually 22,000 to 31,000 cleaned seeds per kilogram (10,000 to 14,000/lb) *(25)*. Most seeds of ash have dormant embryos and require cool, moist stratification to germinate *(25)*. They have medium to high germination and persistent viability. Germination is best and seedlings are most abundant on moist or wet soils rich in organic matter. Germination is scanty in sandy or gravelly stream bottoms where seeds are carried away by floods *(22)*.

Seedling Development—Germination is epigeal. Seedlings grow in height rapidly in rich soils and slowly in poor soils *(22)*. They are somewhat tolerant of shade when quite young *(16)*. Growth is rapidly checked by drought, but seedlings survive drought well *(21)*.

Vegetative Reproduction—Sprouts from stumps are common and vigorous *(2,10,21)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Oregon ash has moderately rapid growth for 60 to 100 years and attains a height of 18 to 24 m (60 to 80 ft) and a d.b.h. of 40 to 75 cm (16 to 30 in) in 100 to 150 years on good sites *(16,22)*. Individuals may grow twice as large and reach 200 to 250 years of age under favorable conditions, although they generally grow slowly after their first hundred years *(22)*. The largest known specimen is 18 m (59 ft) tall and 668 cm (263 in) in circumference *(15)*. In drier parts of its range and at higher elevations, Oregon ash is often smaller than

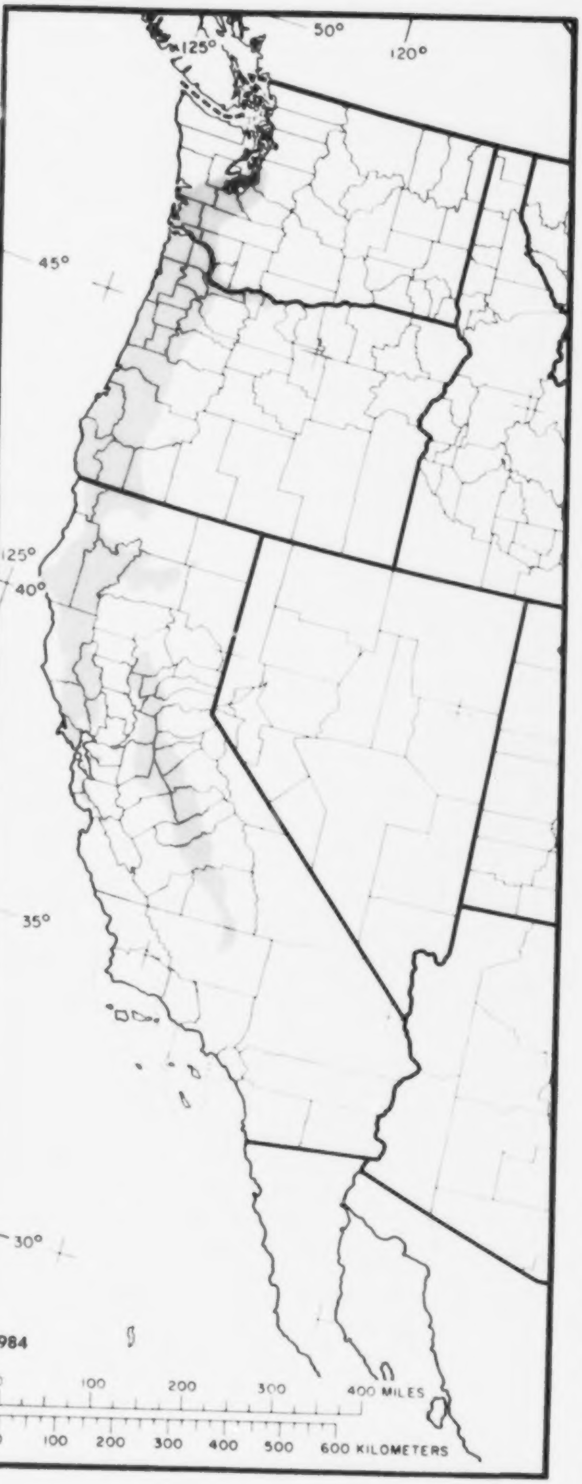

Figure 1—*The native range of Oregon ash.*

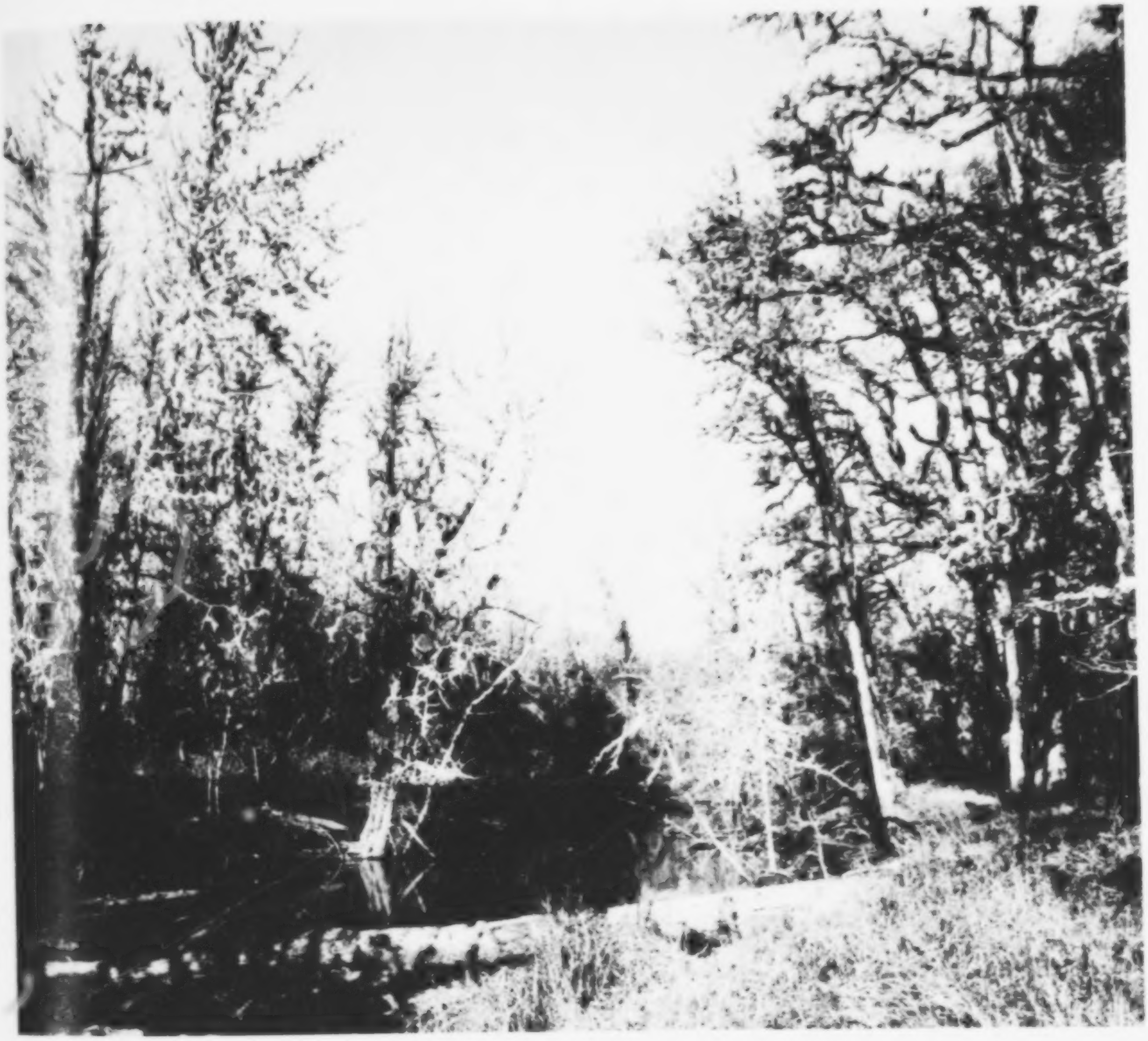

Figure 2—*Oregon ash along a stream in the Willamette Valley, OR. Oregon white oak, a common associate, is present on the right side of the stream.*

8 m (25 ft) tall and 15 to 20 cm (6 to 8 in) in d.b.h. *(22)*.

Rooting Habit—The root system is moderately shallow but very fibrous and wide spreading *(2,21)*. The trees are windfirm *(2,8,21)*.

Reaction to Competition—The species is classed as intermediate in tolerance of shade *(1)*. Individuals self-prune quickly with side shade, and forest-grown trees have long, clean trunks and narrow, short crowns with small branches *(22)*. Overtopped trees respond well to release *(16)*. Open-grown trees on moist sites have short trunks and wide, round-topped crowns with large limbs *(22)*. Oregon ash is often a small, crooked tree on dry sites or at high elevations *(22)*.

Damaging Agents—Oregon ash is attacked by a variety of insects *(5)*. *Thysanocnemis* spp. are small weevils that can destroy 60 percent of a seed crop. They are found throughout the range of the species. Various insects that cause foliage or twig damage harmful to ornamentals but are not considered forest pests are: Arizona ash lace bug *(Leptoypha minor)*, plant bug *(Tropidosteptes pacificus)*, snowy tree cricket *(Oecanthus fultoni)*, and the fall webworm *(Hyphantria cunea)*. The Oregon ash bark beetle *(Leperisinus oregonus)* causes no economic damage but is often abundant in cordwood.

Fungi occurring on Oregon ash that cause leaf spot are *Mycosphaerella effigurata*, *Cylindrosporium fraxini* or *Marssonina fraxini*, *Piggotia fraxini*, *Mycosphaerella fraxinicola*, *Phyllosticta innumera*, and *Cylindrosporium californicum* *(9,24)*. Common powdery mildew *(Phyllactinia guttata)* is found on Oregon ash *(9,19)*. Twig fungi that occur are *Hysterographium fraxini*, *Cytospora ambiens*, and *Nectria cinnabarina* *(9,19,24)*. The true mistletoe *Phoradendron longispicum* is found on Oregon ash. The heart rot *Perenniporia fraxinophilus* attacks older trees and may cause extensive cull *(9,19)*.

Oregon ash is browsed by deer and elk *(17)*.

Special Uses

The most notable use of Oregon ash is for fuel; it splits easily and has high heat value. The symmetrical shape, rapid growth rate, and hardiness of Oregon ash have resulted in its being planted as an ornamental tree and a street tree in cities within its native range, in the Eastern United States, in southwestern British Columbia, and in Europe. It is found in botanical gardens of western and central Europe *(18)*. The wood of Oregon ash is used in its native range for tool handles, sports equipment, boxes, cooperage, and furniture *(2,17)*.

Genetics

No varieties are currently recognized *(11,13)*.

South of the Kern River in California, Oregon ash becomes similar to velvet ash *(Fraxinus velutina)*; anatomical characteristics indicate the possibility of hybridization between the two species *(13)*. Most ash trees in Kern County are intermediate in at least one characteristic *(23)*.

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Fraxinus nigra Marsh. Black Ash

Oleaceae Olive family

Jonathan W. Wright and H. Michael Rauscher

Black ash *(Fraxinus nigra)*, a slow-growing tree of northern swampy woodlands, is the only ash native to Newfoundland. Other common names, swamp ash, basket ash, brown ash, hoop ash, and water ash, indicate some of its characteristics and uses. Many aspects of this tree are unknown because it has never been commercially important. Black ash wood, easily split, has been much used for baskets. The seeds are an important food to game birds, songbirds, and small animals, and the twigs and leaves provide browse for deer and moose.

Habitat

Native Range

Black ash (figs. 1, 2) ranges from western Newfoundland west to southeastern Manitoba and eastern North Dakota; south to Iowa; east to southern Indiana, Ohio, and West Virginia; and north from northern Virginia to Delaware and New Jersey.

Climate

Black ash grows in a humid climate. Average annual precipitation ranges from 510 to 1140 mm (20 to 45 in), 380 to 640 mm (15 to 25 in) of which occurs during the warm season. Average January and July temperatures are from -18° to 0° C (0° to 32° F) and 18° to 21° C (65° to 70° F), respectively. Annual snowfall ranges from 76 to 254 cm (30 to 100 in), and the average frost-free season is from 80 to 180 days.

Soils and Topography

Black ash typically grows in bogs, along streams, or in poorly drained areas that often are seasonally flooded. It is most common on peat and muck soils but also grows on fine sands underlain by sandy till or on sands and loams underlain by lake-washed clayey till *(5,9)*. Although this species can tolerate semistagnant conditions, for best growth it is important that the water be moving so the soil will be aerated even though saturated. Soils suitable for black ash are common in Canada and the northern States. In Indiana, such soils are most common in glaciated areas and in the White River Valley *(4)* but in Pennsylvania, they most frequently occur south of the glaciated areas. These soils are most commonly found in the orders Histosols and Entisols. Black ash is tolerant of a wide range of pH conditions, from 4.4 to 8.2 *(7)*.

In the northern part of its range, black ash is found from sea level to the highest elevations. In the southern part of its range, however, it grows only above 610 m (2,000 ft) in elevation.

Associated Forest Cover

Black ash is an important species of the forest cover type Black Ash–American Elm–Red Maple (Society of American Foresters Type 39). It is a common associate of Northern White-Cedar (Type 37) and a minor associate of Balsam Fir (Type 5), Black Spruce (Type 12), Hemlock–Yellow Birch (Type 24), and Tamarack (Type 38) *(5)*.

Shrubs most commonly associated with black ash are speckled alder *(Alnus rugosa)*, red-osier dogwood *(Cornus stolonifera)*, bog-laurel *(Kalmia polifolia)*, labrador-tea *(Ledum groenlandicum)*, poison-sumac *(Toxicodendron vernix)*, willows *(Salix* spp.), low sweet blueberry *(Vaccinum angustifolium)*, highbush blueberry *(V. corymbosum)*, small cranberry *(V. oxycoccus)*, and common winterberry *(Ilex verticillata)* *(4,5)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Black ash is polygamous; its flowers are small and inconspicuous. They appear in May or June at about the same time as, or just before, the leaves. The fruit is an elongated, winged, single-seeded samara that is borne in terminal or axillary clusters. It ripens from June to September *(12)*.

Seed Production and Dissemination—Seeds are dispersed from July to October. A 25-year seed crop survey of 19 tree species in northeastern Wisconsin showed that black ash produced good seed crops 28 percent of the years, medium seed crops 4 percent of the years, and poor seed crops 68 percent of the years. Of the 19 northern forest tree species investigated, black ash registered the longest period of poor seed crop, 7 years *(7,12)*.

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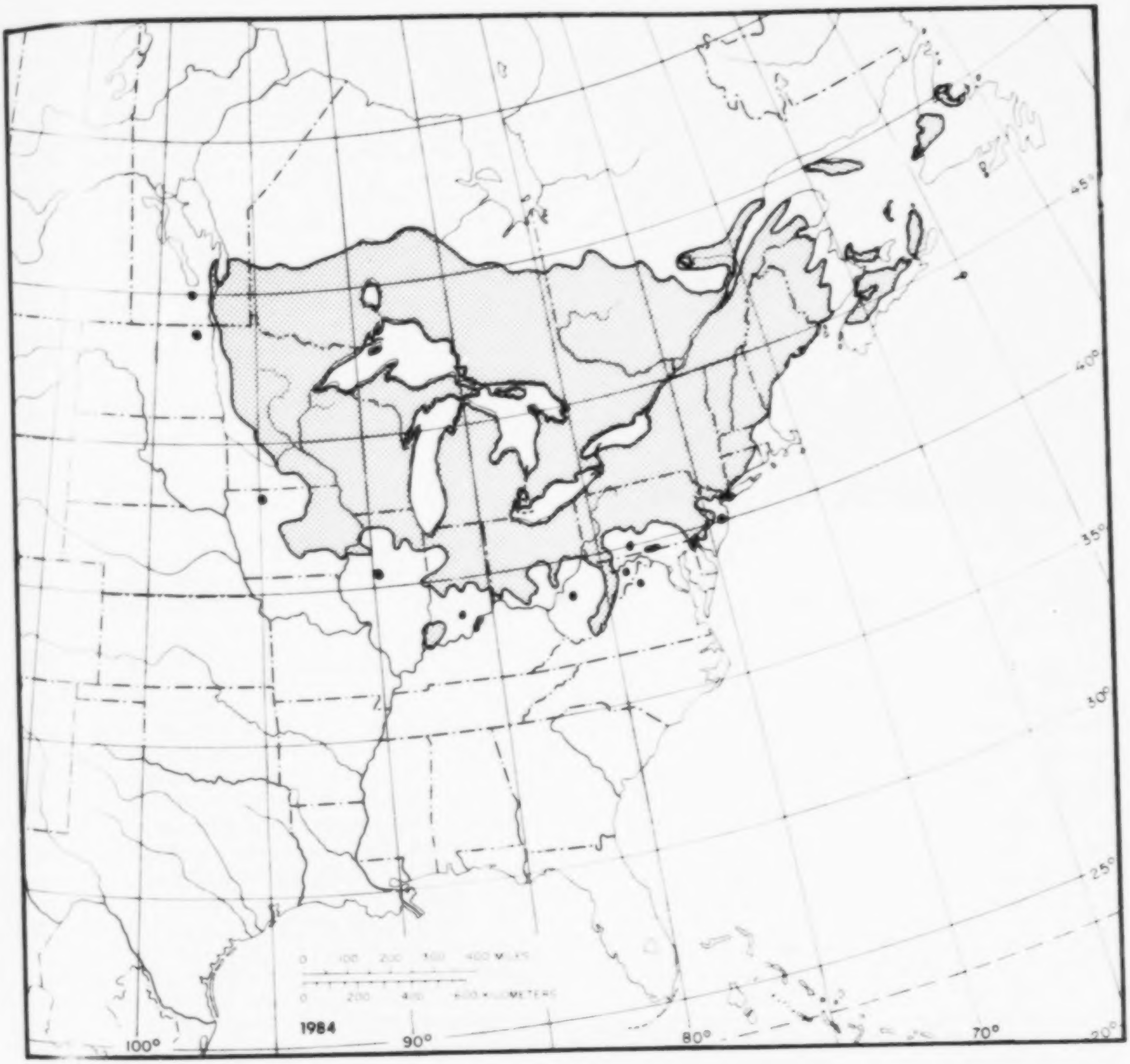

Figure 1—*The native range of black ash.*

Among the ashes, black ash is about average in seed production. Seeds average between 27.7 and 36.[illegible] kg/45.4 kg of fruit (61 and 80 lb 100/lb). When cleaned, there are 13,500 to 20,900 seeds per kilogram (6,100 to 9,500 lb) or an average of 17,900 kg ([illegible],100 lb) *(12)*.

Black ash seeds show dormancy because they have immature embryos, respiratory enzymes in the endosperm, and impermeable seedcoats. Dormancy can be overcome with moist stratification in sand for 2 to 3 months at room temperatures (20° C or 68° F) followed by stratification for 3 months at a temperature slightly above freezing (5° C or 41° F). The embryos mature and seedcoats become permeable during warm stratification and inhibitors disappear during cold stratification *(12,13)*.

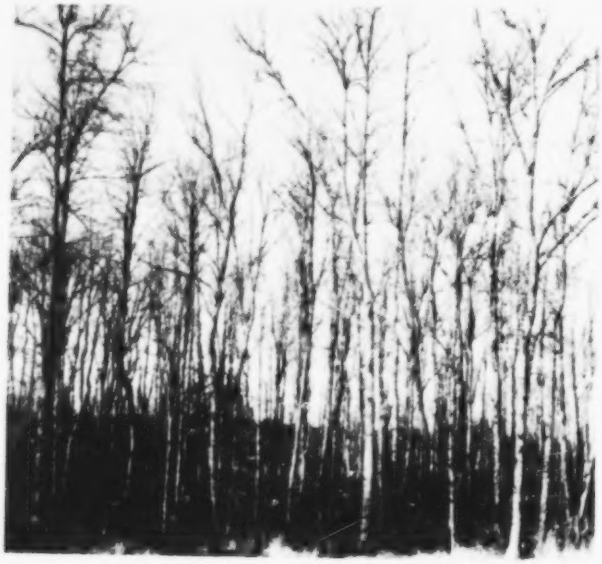

Figure 2—*Black ash boles support small open crowns and are inclined to be poorly shaped.*

Seedling Development—Because of dormancy, black ash seed does not normally germinate under natural conditions until the second year. In the nursery, ash seeds may be planted in the fall soon after they are collected and then mulched with burlap or straw until spring, and covered with 6 to 20 mm (0.25 to 0.75 in) of soil. Standard practice is to broadcast or drill seeds to achieve a nursery bed density of about 110 to 160 seedlings per square meter (10 to 15 ft). Germination is epigeal and usually occurs during the second year. Seedlings usually are outplanted as 1–0 stock, sometimes 2–0 in North America *(12)*. Black ash seeds may remain viable for 8 years or more under natural conditions.

In natural stands, black ash seedlings commonly grow more slowly than do those of associated species such as American elm *(Ulmus americana)* and red maple *(Acer rubrum)*. Young black ash sprout readily from stumps.

Sapling and Pole Stages to Maturity

Growth and Yield—Black ash is a small tree. The largest one on record is growing in Bath, OH, and is 26.5 m (87 ft) tall and 148 cm (58.3 in) in d.b.h., with a crown spread of 18.3 m (60 ft) *(10)*. More commonly, the largest trees reach a height of 18 to 21 m (60 to 70 ft) and a diameter of 30 to 61 cm (12 to 24 in). In many forests, the largest trees are only 20 to 25 cm (8 to 10 in) in d.b.h.

As would be expected of a species that grows in areas with a high water table, black ash has a relatively slow growth rate. Site index at base age 50 years ranges from 15 to 24 m (50 to 80 ft) in northern Wisconsin and Michigan *(2)*. Forest survey data from 20 counties in northern Minnesota indicate that black ash is only about 80 percent as tall at age 50 as is balsam fir *(Abies balsamea)* on the same site *(3)*. In many Michigan bogs, black ash–red maple stands grow only 9 to 11 m (30 to 35 ft) tall before they are replaced by northern white-cedar *(Thuja occidentalis)* *(6)*.

In a Minnesota study *(11)*, freshly fallen black ash leaves were found to contain larger amounts of calcium, magnesium, nitrogen, and ash than other hardwoods. The phosphorus content of the foliage was similar to that of most other hardwoods.

Rooting Habit—Black ash has a shallow and fibrous root system *(8)*, particularly well adapted to growth under conditions of high soil moisture.

Reaction to Competition—Black ash is classed as intolerant of shade *(8)*.

Damaging Agents—A study based on an extensive survey of defects in Ontario forest trees concluded that black ash is the most defective of eight deciduous species. The fungi most frequently associated with trunk rot and butt rot of black ash were *Stereum murrayi* and *Armillarea mellea*, respectively *(1)*. The oystershell scale *(Lepidosaphes ulmi)* occasionally kills reproduction and older trees. Leaf spot *(Mycosphaerella effigurata)*, anthracnose *(Gloeosporium aridum)*, rust *(Puccinia peridermiospora)*, and canker *(Nectria galligena)* cause damage to black ash similar to that reported for white ash *(Fraxinus americana)*. The spongy white (heartwood) rot caused by *Polyporus hispidus* enters through wounds and is usually found in the upper tree trunk. It is occasionally a serious problem; in one Minnesota stand, it caused degrade of lumber in 5 percent of the trees *(14)*. Deer browse heavily on young black ash and if poplars are scarce, beaver will cut down ash between 25 and 51 cm (10 to 20 in) in stump diameter.

Genetics

There are no known races or hybrids of black ash.

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Fraxinus pennsylvanica Marsh. Green Ash

Oleaceae Olive family

Harvey E. Kennedy, Jr.

Green ash *(Fraxinus pennsylvanica)*, also called red ash, swamp ash, and water ash, is the most widely distributed of all the American ashes. Naturally a moist bottom land or stream bank tree, it is hardy to climatic extremes and has been widely planted in the Plains States and Canada. The commercial supply is mostly in the South. Green ash is similar in property to white ash and they are marketed together as white ash. The large seed crops provide food to many kinds of wildlife. Due to its good form and resistance to insects and disease, it is a very popular ornamental tree.

Habitat

Native Range

Green ash (fig. 1) extends from Cape Breton Island and Nova Scotia west to southeastern Alberta; south through central Montana, northeastern Wyoming, to southeastern Texas; and east to northwestern Florida and Georgia.

Climate

The climate within the range of green ash is subhumid to humid, with the following ranges: Annual precipitation from 380 to 1520 mm (15 to 60 in), warm season precipitation from 250 to 890 mm (10 to 35 in); average January temperature of -18° to 13° C (0° to 55° F); average July temperature of 18° to 27° C (65° to 80° F); snowfall from 0 to 254 cm (0 to 100 in); average length of frost-free season 120 to 280 days.

Soils and Topography

Like most trees, green ash grows best on fertile, moist, well-drained soils. It is probably the most adaptable of all the ashes, growing naturally on a range of sites from clay soils subject to frequent flooding and overflow to sandy or silty soils where the amount of available moisture may be limited *(24)*. Natural stands of green ash are almost completely confined to bottom lands, but the species grows well when planted on moist upland soils. It thrives when planted on medium- to coarse-textured upland sands and loams from North Dakota to Texas where soils had good moisture and neutral to alkaline reactions. Green ash most commonly is found on alluvial soils along rivers and streams and less frequently in swamps *(25)*. It lines the watercourses in the western parts of its range where rainfall is insufficient to support upland growth. It is common on land subject to flooding and can remain healthy when flooded for as long as 40 percent of the time during a growing season. Green ash grows on soils most common to the orders Inceptisols and Entisols.

In fertilizer experiments, green ash was tolerant of soil alkalinity but showed severe chlorosis when grown on a soil with a pH of 8.1 *(25)*. Culture-species tests on a riverfront site in Mississippi have shown that ash grew well on a silt-loam soil with a pH ranging between 7.5 and 8.0.

Other studies have shown the importance of soil characteristics to tree growth. Growth was much better on soils that had not been cultivated than on ones that had been in cultivation *(7)*. The longer an area had been in cultivation or the more severely eroded the A horizon, the poorer the growth of green ash. Forest sites support better growth than old field sites, probably because of suitable mycorrhizae and organic matter in the forest soils.

Green ash has been planted on spoil banks resulting from strip-mining *(25)*. These soils usually are highly acidic. Survival generally has been high, but annual growth rates of only about 0.3 m (1 ft) have been reported. Studies in Arkansas on sandy loam soils with pH ranging from 5.0 to 5.4 have shown excellent survival and growth rates of 1.5 to 1.8 m (5 to 6 ft) per year.

Associated Forest Cover

Green ash is an integral part of the forest cover type Sugarberry–American Elm–Green Ash (Society of American Foresters Type 93) and is an associated species in the following types *(22)*:

16	Aspen
26	Sugar Maple–Basswood
42	Bur Oak
52	White Oak–Black Oak–Northern Red Oak
62	Silver Maple–American Elm
63	Cottonwood
65	Pin Oak–Sweetgum
87	Sweetgum–Yellow-Poplar
88	Willow Oak–Water Oak–Diamondleaf (Laurel) Oak

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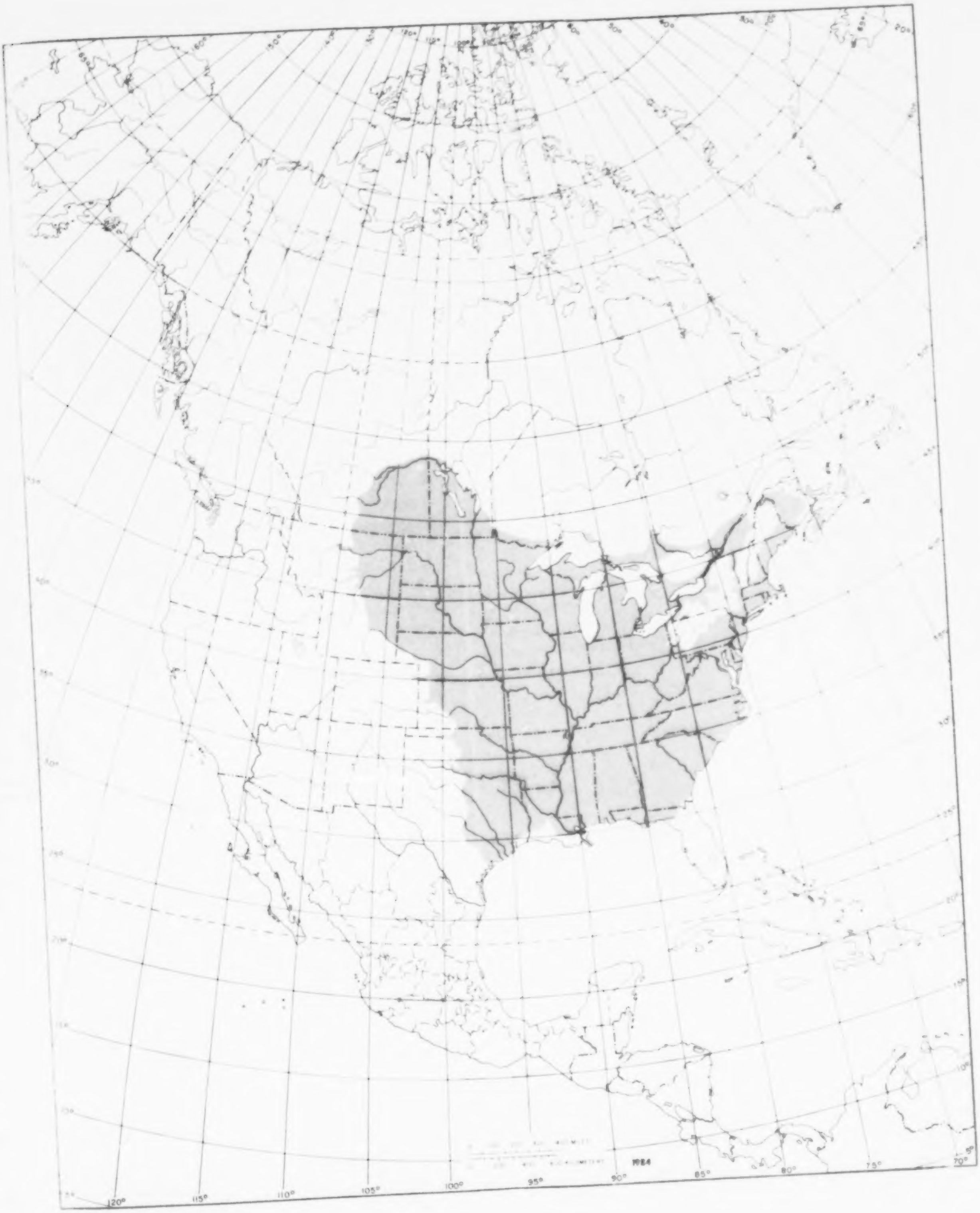
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Figure 1—*The native range of green ash.*

89	Live Oak
91	Swamp Chestnut Oak-Cherrybark Oak
92	Sweetgum-Willow Oak
94	Sycamore-Sweetgum-American Elm
95	Black Willow
96	Overcup Oak-Water Hickory
101	Baldcypress
102	Baldcypress-Tupelo
103	Water Tupelo-Swamp Tupelo

Species most commonly associated with green ash are boxelder *(Acer negundo)*, red maple *(A. rubrum)*, pecan *(Carya illinoensis)*, sugarberry *(Celtis laevigata)*, sweetgum *(Liquidambar styraciflua)*, American sycamore *(Platanus occidentalis)*, eastern cottonwood *(Populus deltoides)*, quaking aspen *(P. tremuloides)*, black willow *(Salix nigra)*, willow oak *(Quercus phellos)*, and American elm *(Ulmus americana)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Green ash is dioecious. The small, usually inconspicuous flowers appear in the spring, with or just before the leaves, in terminal or axillary clusters *(4)*. Flowers are generally borne over the entire outer part of the live crown. Usually, flowering starts when trees are 8 to 10 cm (3 to 4 in) d.b.h. and 6 to 8 m (20 to 25 ft) tall. A high percentage of the male and female trees bear flowers annually, and many female trees bear fruit each year.

Flowers may appear as early as March or April in Florida and from late April to early May in the northern part of its range *(25)*. Male flowers require 1 to 2 weeks to pass from the enlarged winter condition to completion of pollen shedding. Individual trees shed pollen over an interval of 3 to 4 days. Within a stand, range among individual trees in onset of pollen shedding is only 2 to 3 days. The pollen is disseminated by wind and is dispersed relatively short distances, most of it falling within 61 to 91 m (200 to 300 ft) of the source.

Flower bud enlargement starts a few days later on female trees than on male *(25)*. The stigmas of the female flowers are receptive as soon as they emerge from the bud and remain receptive for about a week. Receptivity appears to end just before the stigmas start to wither. The female flowers and young fruit are very sensitive to late spring frosts.

Within a month after pollination, the samaras developing from fertilized flowers reach mature size. Ash fruits are elongated, winged, single-seeded samaras borne in clusters. Unpollinated flowers or flowers pollinated by an incompatible ash species drop off within the first month. Growth and ripening of embryos lag behind growth of samaras and are not completed until late September or early October.

Physiological maturity of green ash seeds can be related to a fully elongated embryo that fills the entire embryonic cavity. When ripe, the embryo should be about 10 mm (0.4 in) long and slightly less than 1 mm (0.04 in) in diameter. Mature embryos have firm, white tissues that break crisply. Physical characteristics indicating seed maturity can be utilized by workers in the field during seed collections *(3)*. Color change in the samaras, from green to yellow or brown, is not complete until after the embryo is fully grown. Samples picked in mid-October in central Mississippi gave excellent germination though samaras were still slightly green. While samaras are still green, they may contain as much as 50-percent moisture, and care must be taken to prevent seed lots from overheating. A little heat damage at this stage may significantly reduce seed quality, especially if long-term storage is contemplated. In seed collections, especially bulk collections, complete change of samaras to a brown color probably is a safer index to maturity than size of the embryo.

Seed Production and Dissemination—Green ash seeds start to fall as soon as they ripen and continue to fall into the winter *(25)*. Most seeds are dispersed by wind within short distances of the parent tree. Some dispersal by water also may occur, but the importance of water as a long-distance dispersal agent is unknown.

Seed clusters can be collected from trees by hand or with pruners and seed hooks. Fully dried samaras also may be shaken or whipped from limbs of standing trees onto plastic sheets spread under the trees. Fruit should be spread in shallow layers for complete drying, especially when collected early. Dried clusters may be broken apart by hand, by flailing in sacks, or by processing through a macerator. Seeds should be dried to 7- to 10-percent moisture content for storage. No loss in viability for 7 years was found when green ash seeds were stored in sealed containers at 5° C (41° F) with a seed moisture content of 7 to 10 percent.

The epigeal germination may occur in the spring following seedfall, or seeds may lie dormant in the litter for several years before germinating. Dormancy is apparently due to both internal factors and to seedcoat effects *(3,4)*. For the nursery, dormancy may be overcome by cold, moist stratification in a suitable medium, or simply storing in containers of water. Both methods should be used at temperatures of 2°

to 4° C (35° to 40° F) for 90 to 120 days. Seeds may be sown in fall and allowed to stratify in the nursery bed.

Seeds should be sown in nursery beds at approximately 80 to 100/m (25 to 30/ft) of row with rows 15 to 30 cm (6 to 12 in) apart *(25)* and covered with burlap or greenhouse shade cloth until germination starts. Seedbed densities of 110 to 130/m² (10 to 12/ft²) are recommended for green ash to produce high-quality seedlings.

Seedling Development—Under good nursery conditions in the northern part of its range, seedlings grow about 30 cm (12 in) in height the first year and another 46 cm (18 in) the second year. In the southern part of the green ash range, nurseries can produce seedlings 0.8 to 0.9 m (2.5 to 3.0 ft) tall the first growing season.

Uninjured nursery seedlings usually develop no side branches during the first year. On vigorous seedlings, the uppermost one or two pairs of lateral buds develop into branches during the second year.

Apical dominance usually is strong enough in vigorous, uninjured open-grown trees so that they often have a single, straight stem until they are 5 m (15 ft) or more tall. If this dominance is lost by the removal of a terminal bud, the uppermost lateral branch quickly takes over and reasserts dominance over the lower branches *(25)*. In slow-growing shaded specimens, the tendency for quick assertion of apical dominance following deer nipping or other damage to a terminal bud is much less pronounced. As a consequence, understory seedlings frequently have poor form.

Vegetative Reproduction—Stumps of sapling- and pole-size green ash sprout readily. Studies in Mississippi have shown ash, as sprouts, to be one of the dominant species in bottom-land clearings *(11,13)*. Dominants among the ash sprouts were 3.8 cm (1.5 in) d.b.h. and 5 m (15 ft) tall after five growing seasons.

Cuttings made from 1-0 seedlings or 1-year-old sprouts root easily under greenhouse and field conditions *(25)*. Cuttings may be planted horizontally under the soil or vertically with good results (fig. 2) *(14,15)*. However, no practical way to root cuttings from older trees has yet been found. Green ash can be successfully bench-grafted or field-grafted *(2,18)*. Understocks can be stored by severely root-pruning young seedlings and heeling them in by groups of 50 to 100. Most of the seedlings remain alive but grow so little that they supply an assortment of small understocks whenever needed.

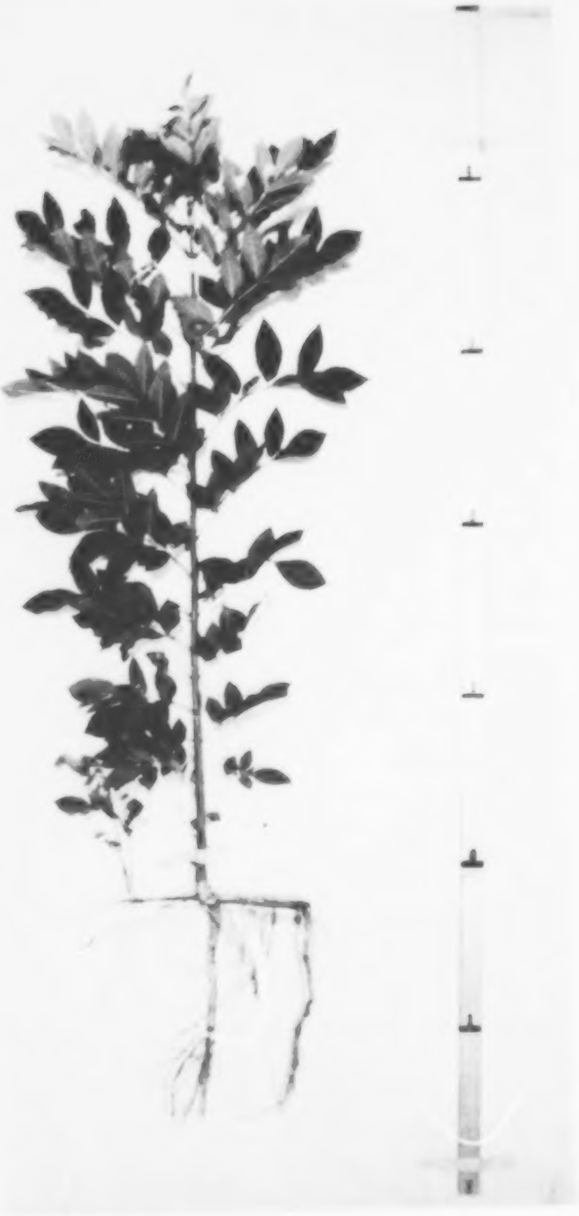

Figure 2—*Stem and root development of a horizontally planted green ash cutting after one growing season.*

Sapling and Pole Stages to Maturity

Growth and Yield—In shelterbelts in the Great Plains, green ash averaged 0.4 m (1.3 ft) per year height growth for the first 6.5 years *(25)*. Open-grown trees planted on a fertile soil in Pennsylvania grew 14 to 17 m (45 to 55 ft) tall and 20 to 30 cm (8 to 12 in) in d.b.h in 21 years.

In most areas in the northern part of its range, green ash reaches heights of 15 to 18 m (50 to 60 ft) and breast-high diameters of 46 to 61 cm (18 to 24 in). On good sites in the southern part of its range, trees attain a height up to 37 m (120 ft) and a d.b.h. of 61 to 76 cm (24 to 30 in) *(20)*. Diameter growth of dominant crop trees in well-stocked, managed stands is about 6 to 8 cm (2.5 to 3.0 in) in 10 years *(5)*.

Little data exist on growth rates and volumes of trees grown under natural stand conditions. Probably the best information available is contained in results of research conducted in Georgia *(6)*. Four sites included in the study ranged from well-drained sandy loams on levees or terraces to poorly drained, wet, silty flats. Green ash was the dominant species in these stands, comprising about 80 percent of the total stand basal area. Stand ages ranged from 27 to 65 years. Average stand heights for green ash sawtimber ranged from 24 m (78 ft) in the 27-year-old stand to 35 m (116 ft) in the 65-year-old stand. Volume growth ranged from 2.7 to 4.6 m^3/ha (39 to 65 ft^3/acre) per year. Growth was related to stand age with better growth rates occurring in the younger stands. Merchantable sawtimber volume ranged from 104.4 m^3/ha (1,491 ft^3/acre) in the 27-year-old stand to 175.8 m^3/ha (2,511 ft^3/acre) in the 65-year-old stand. In addition to sawtimber, pulpwood volumes from tops and small trees ranged from 144.8 m^3/ha (23 cords/acre) in the younger stand to 245.6 m^3/ha (39 cords/acre) in the older stand.

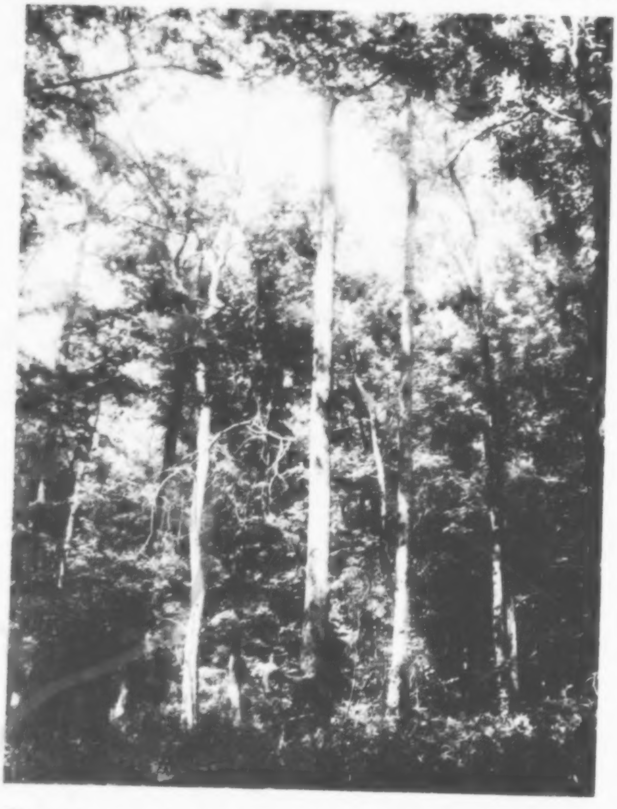

Figure 3—*A good natural stand of green ash on Falaya-Waverly soil.*

Green ash on most sites in the southern part of its range is characterized by a clear, straight bole for about half the total height (fig. 3) *(6)*. Above this point the stem often forks or crooks and has large branches that degrade the lumber. Merchantable height for saw logs averages about two 5-m (16-ft) logs. Merchantable height for pulpwood to a 10-cm (4-in) top may extend to 12 m (40 ft) in younger stands. Its pioneer nature and ability to grow rapidly in relatively pure, even-aged stands indicate green ash is well suited for plantation management. Studies in Mississippi and Arkansas have shown that green ash grows about 1.2 to 1.5 m (4 to 5 ft) in height and 13 mm (0.5 in) in d.b.h. the first 5 to 10 years under plantation management (fig. 4).

Natural stands appear to support sufficient volume to allow commercial thinnings at 25 to 30 years *(6)*. To ensure reasonable volume production and reduce epicormic branching in the residual stand, basal area should not be reduced below 23.0 to 27.6 m^2/ha (100 to 120 ft^2/acre). This should be represented by about 250 to 300 trees/ha (100 to 120 trees/acre).

Rooting Habit—Root systems were studied in North Dakota on a Fargo clay soil, with a 0.3-m (1-ft) layer of black surface soil overlaying a light-colored, calcareous, clayey soil with no hardpan *(25)*. The soil

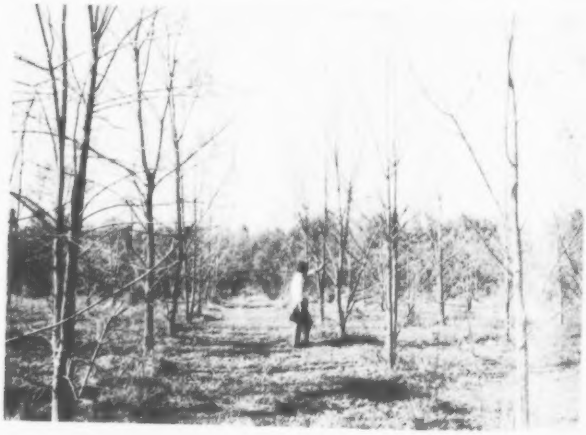

Figure 4—*Five-year-old plantation-grown green ash.*

was poorly drained and wet in the spring; later in the growing season the water table was at a depth of about 5 m (15 ft) or more. Roots had extended laterally for 15 m (48 ft) and 1.1 m (3.6 ft) downward; they were about equally distributed in the upper 0.9 m (3 ft) of soil. Excavations of other root systems have shown green ash roots to penetrate about 1 m (3.2 ft) deep in sandy and clay soils and 1.4 m (4.5 ft) deep along the edges of sloughs. In the southern part of its range, green ash has a root system that is typically saucer-shaped with no distinct taproot; roots penetrate to depths of 0.9 to 1.2 m (3 to 4 ft). The extensive root system of this species makes it relatively windfirm.

Green ash seedlings, and probably older trees, have certain rooting habits or adaptations that enable them to withstand flooding *(1,16,21)*. Young green ash *(8)* has been shown to have the ability under flooded conditions to regenerate new secondary roots from the primary root, develop adventitious water roots on the submerged stem, accelerate anaerobic respiration rate in the absence of oxygen, and oxidize its rhizospheres. These root adaptations enable it to withstand flooding regimes of several months during the dormant and early growing season that would kill other species *(9,10,25)*. Specific gravity has been shown to be related to flooding in some hardwoods *(19)*.

Reaction to Competition—Green ash varies from intolerant to moderately tolerant to shade in the northern part of its range. It comes in early in succession on alluvial soils, either as a pioneer species or following cottonwood, quaking aspen, or black willow *(25)*. It is less able to maintain its position in the crown canopy than some of its more rapidly growing associates such as red maple and American elm.

In the southern part of its range, green ash would be considered tolerant when young and moderately tolerant as it grows older. Studies have shown that advanced reproduction of green ash can be maintained in the understory for more than 15 years *(12)*. Green ash may not grow more than 15 cm (6 in) in height yearly, with 12- to 15-year-old trees being 4 to 5 m (12 to 15 ft) tall and 2.5 cm (1 in) in diameter. However, these trees respond well to release and outgrow many of their competitors *(13)*. Other studies of green ash in plantations, where various levels of cultural treatments were applied, showed that green ash could tolerate competition from weeds and vines better than any of the 6 to 10 other species tested *(17)*. Overall, green ash may most accurately be classed as tolerant of shade.

Damaging Agents—Many insects feed at least occasionally on green ash. One of the most serious is the oystershell scale *(Lepidosaphes ulmi)*, which is distributed throughout the Northeast and can cause serious damage among seedlings and small trees. The carpenterworm *(Prionoxystus robiniae)* bores into the heartwood of large branches and trunks, permitting the entrance of fungi. The brownheaded ash sawfly *(Tomostethus multicinctus)* and the blackheaded ash sawfly *(Tethida barda)* occasionally cause serious damage to shade trees. The ash borer *(Podosesia syringae)* damages the stems of trees of all sizes, causing lumber degrade in timber-sized trees and contributing to decline and mortality in shelterbelt plantings *(23,25)*.

Several diseases are of general importance. The fungus *Mycosphaerella fraxinicola* creates a leaf spot which may cause premature defoliation of young trees. Anthracnose *(Gloeosporium aridum)* also causes premature defoliation. A rust caused by *Puccinia peridermiopora* results in distortion of petioles and small twigs. Several rots cause minor damage in green ash. In Texas and Oklahoma, green ash has shown intermediate susceptibility to a root rot caused by *Phymatotrichum omnivorum (25)*.

Young trees are subject to damage from deer browsing, and rabbits may sever the stems.

Special Uses

Green ash wood, because of its strength, hardness, high shock resistance, and excellent bending qualities, is used in specialty items such as tool handles and baseball bats but is not as desirable as white ash. It is also being widely used in revegetation of spoil banks created from strip mining *(25)*. Green ash is very popular as a shade tree in residential areas because of its good form, adaptability to a wide range of sites, and relative freedom from insects and diseases. Seeds are used for food by a number of game and nongame animals and birds.

Genetics

Population Differences

Green ash is composed of three or more geographic ecotypes. The trees belonging to these ecotypes are easily distinguishable when growing under uniform conditions in a nursery but not when growing naturally. For that reason, they have not been given Latin varietal or subspecific names.

Three different ecotypes were evident in the Great Plains (25). The population from the arid, northwestern part of the green ash range was more drought resistant than that from the more moist central Great Plains. As compared with the Coastal Plain ecotype, the Northern States ecotype grew more slowly, had greener petioles, was more winter hardy, and was less subject to leaf damage by fall frosts. These ecotypes may or may not be identical with those from the Eastern United States.

Hybrids

Attempts have been made to artificially cross green ash with other ash species. Only the cross of green ash with velvet ash (*Fraxinus velutina*) was consistently successful, yielded viable seed, and produced identifiable hybrids that grew as fast as the eastern parent. The other crosses yielded no identifiable hybrids.

The pumpkin ash (*Fraxinus profunda*) is a rare hexaploid (2n = 138 chromosomes) species of the Coastal Plain and Mississippi Valley (*25*). Its leaves, twigs, flowers, and fruit are larger than those of green ash or white ash but qualitatively similar to one or the other of these two species. The patterns of morphological variation and geographic distribution taken together are strong evidence for the view that pumpkin ash is a true-breeding polyploid derivative of a cross between a diploid green ash and tetraploid white ash.

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Fraxinus profunda (Bush) Bush — Pumpkin Ash

Oleaceae — Olive family

W. R. Harms

Pumpkin ash *(Fraxinus profunda)*, also called red ash, is a large tree of swamps and bottom lands where it often develops a swollen or pumpkin-shaped butt. For management and utilization, it is treated the same as other ashes. The seeds are eaten by birds and deer browse on the branches.

Habitat

Native Range

Pumpkin ash (figs. 1, 2) is found locally along swamp margins and river bottoms, chiefly in the Atlantic Coastal Plain from southern Maryland and southeastern Virginia to northern Florida, and west to Louisiana. It also grows in the Mississippi and Ohio River Valleys from southern Illinois and Indiana, south through southeastern Missouri and northeastern Arkansas. Its range, however, is quite discontinuous.

Climate

Annual precipitation varies from 1020 mm (40 in) in the central part of the range to 1220 mm (48 in) in the east and south. Average rainfall in the growing

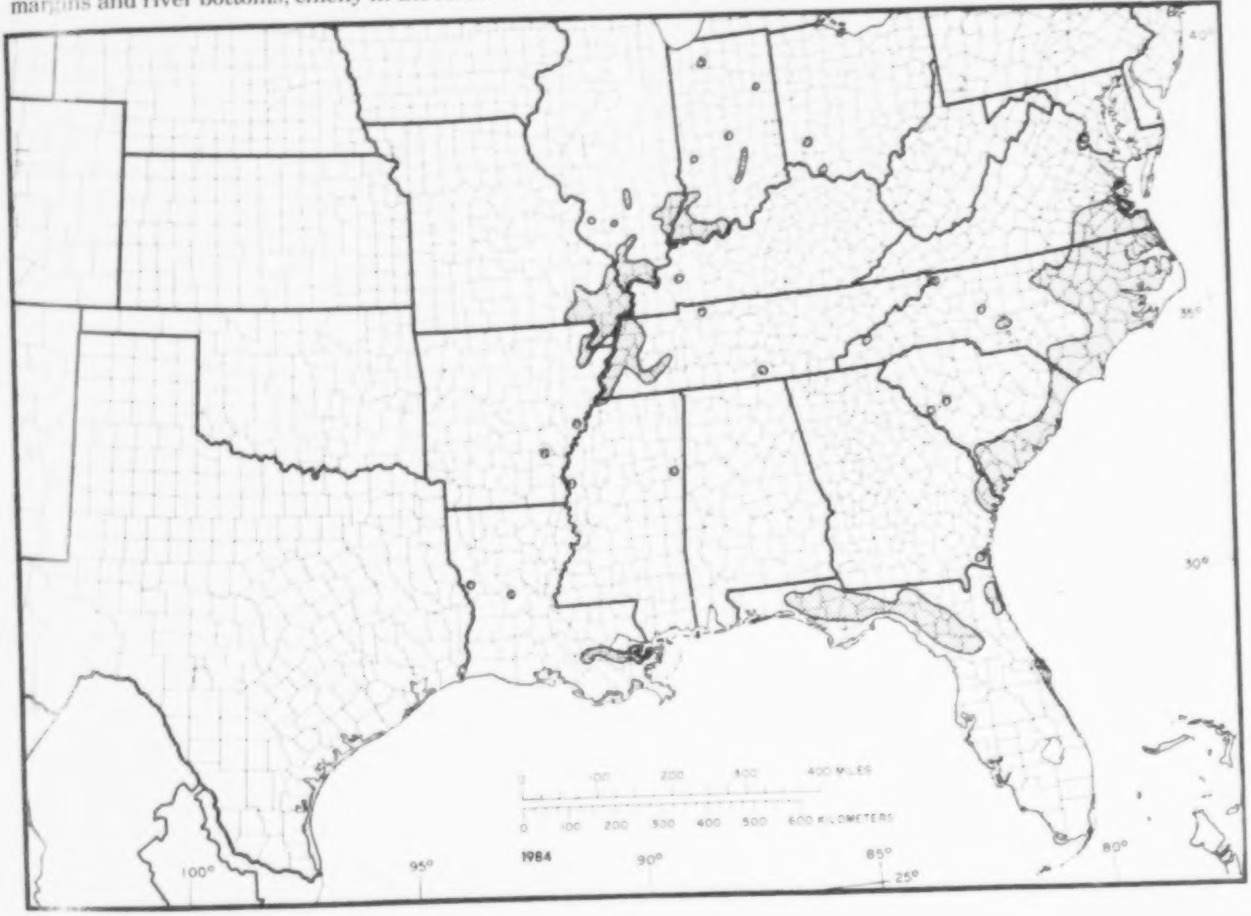

Figure 1—*The native range of pumpkin ash.*

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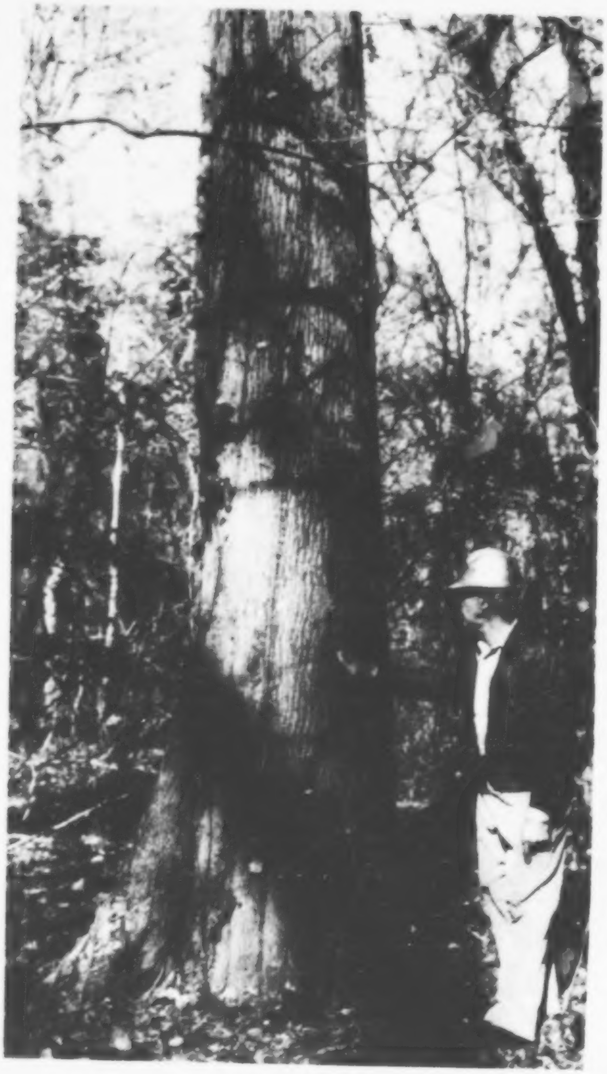

Figure 2—*Pumpkin ash on the Francis Marion National Forest in South Carolina.*

season, March through September, is 660 mm (26 in). The average summer temperature ranges from 27° C (80° F) in the north to 28° C (82° F) in the south, and the average winter temperature ranges from 2° C (35° F) in the north to 16° C (60° F) in the south. The number of frost-free days extends from 180 in the central region to 270 in the southern region.

Soils and Topography

Pumpkin ash is found on wet to very wet sites where, in years of normal rainfall, surface water stands well into the growing season. Sites include the margins of swamps and deep sloughs, very low, poorly drained flats of the major river floodplains, swamps of tidal estuaries, margins of coastal marshes, and the deeper, more extensive depressions of the Coastal Plain. The soils are mineral and usually range in texture from silt loam to clay loam. Swamps and depressions usually have a surface of muck or shallow peat. Soils in the central part of the range belong to the Alfisols and Entisols, while those in the east and south include the Spodosols and Ultisols *(5)*.

Associated Forest Cover

Pumpkin ash is listed as a minor component of three forest cover types: Baldcypress (Society of American Foresters Type 101), Baldcypress–Tupelo (Type 102), and Water Tupelo–Swamp Tupelo (Type 103) *(1)*. Other species associated with pumpkin ash are red maple *(Acer rubrum)* and silver maple *(A. saccharinum)*, blackwillow *(Salix nigra)*, Carolina ash *(Fraxinus caroliniana)*, swamp cottonwood *(Populus heterophylla)*, water-elm *(Planera aquatica)*, and water locust *(Gleditsia aquatica)*. On the better drained sites, overcup oak *(Quercus lyrata)*, swamp chestnut oak *(Q. michauxii)*, willow oak *(Q. phellos)*, water oak *(Q. nigra)*, water hickory *(Carya aquatica)*, American elm *(Ulmus americana)*, green ash *(Fraxinus pennsylvanica)*, Nuttall oak *(Q. nuttallii)* in the Mississippi River bottoms; laurel oak *(Q. laurifolia)*, sweetgum *(Liquidambar styraciflua)*, persimmon *(Diospyros virginiana)*, and sweetbay *(Magnolia virginiana)* are also present. Among the understory trees and shrubs commonly found in the deep swamps are buttonbush *(Cephalanthus occidentalis)*, swamp-privet *(Forestiera acuminata)*, Virginia-willow *(Itea virginica)*, swamp dogwood *(Cornus stricta)*, swamp cyrilla *(Cyrilla racemiflora)*, possumhaw *(Ilex decidua)*, swamp rose *(Rosa palustris)*, and poison-sumac *(Toxicodendron vernix)*; and such species as dahoon *(Ilex cassine)*, yaupon *(I. vomitoria)*, southern bayberry *(Myrica cerifera)*, and lyonia fetter bush *(Lyonia lucida)* in the shallower upland swamps.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pumpkin ash is dioecious, flowering in April and May before the leaves flush. The fruit is a winged, single-seeded samara and is borne in clusters. Pumpkin ash has the largest seed of the native ash species; seeds average 6.1 to

7.1 cm (2.4 to 2.8 in) in length and 9 mm (0.35 in) in width *(4)*.

Seed Production and Dissemination—Seed production begins at an early age; the youngest seed-bearing age has been reported to be 10 years. The seeds mature in late summer, and fall between October and December. Most of the seeds are wind dispersed, though some dispersal by water occurs and may be important to regeneration under some conditions. Seeds remain viable in water for several months. There are no published data on abundance and periodicity of seed crops; however, pumpkin ash is apparently not a prolific seeder *(6)*. Number of cleaned seed averages 7,050/kg (3,200/lb).

Seedling Development—Germination is epigeal. Pumpkin ash, in common with its associate green ash, reproduces best on bare, moist soil in openings. Seedlings are moderately shade tolerant and grow rapidly provided that the site is not totally preempted by ground cover or a dense overstory. They are tolerant of saturated soil conditions *(2)*.

Vegetative Reproduction—Sapling and pole-size ash sprout readily. The sprouts grow rapidly and can rise above seedlings of most other species very quickly *(3)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Pumpkin ash is a large tree, reaching a height of 40 m (130 ft) and a diameter at breast height of 173 cm (68 in) on the best sites. On the wettest sites it commonly develops a swollen or pumpkin-shaped butt, hence its name. There are no published growth or yield data, and in practice it has not been practical to distinguish it from green ash either for management purposes or in its utilization *(3)*.

The species can be readily planted. Unpublished records for a plantation in the Mississippi Delta show that trees planted on a cleared site at a square spacing of 3.7 m (12 ft) averaged 6.7 m (22 ft) in height and 8.9 cm (3.5 in) in d.b.h. at age 6.

Rooting Habit—There is no published information on rooting habits.

Reaction to Competition—Pumpkin ash is tolerant of shading when young and grows more rapidly than green ash. It becomes less tolerant as it ages. Overall, it is most accurately classed as intermediate in shade tolerance. Pumpkin ash, along the margins of swamps and sloughs, grows very slowly. At somewhat higher elevations, where the soils are better drained, it grows more rapidly *(6)*.

Damaging Agents—Pumpkin ash is very susceptible to fire. It is moderately susceptible to dieback during drought on the wettest sites. Upper stem heartrot *(Lentinus tigrinus)* may be severe in overmature trees. There are no published data on specific insect or disease problems *(3)*.

Special Uses

Pumpkin ash produces high-quality factory lumber and dimension material and is an important source of handle and implement stock. The fruits are eaten by wood ducks and many other birds. White-tailed deer browse the young twigs and leaves.

Genetics

Pumpkin ash is considered to be a true-breeding polyploid derivative of a cross between a diploid green ash and a tetraploid white ash. No races or hybrids have been reported *(7)*.

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Gleditsia triacanthos L. Honeylocust

Leguminosae **Legume family**

Robert M. Blair

Honeylocust *(Gleditsia triacanthos)*, also called sweet-locust or thorny-locust, is a moderately fast growing tree commonly found on moist bottom lands or limestone soils. Because it has proven very hardy and tolerant of drought and salinity, it is widely planted for windbreaks and soil erosion control. The thornless variety has been planted to replace the elm in many urban areas. The wood is dense, hard, and durable but used only locally. Honeylocust pods are sweet and eaten by livestock and wildlife. The tree is relatively short lived, reaching the age of 125 years.

Habitat

Native Range

Honeylocust (fig. 1) is found scattered in the East-Central United States from central Pennsylvania westward to southeastern South Dakota, south to central and southeastern Texas, east to southern Alabama, then northeasterly through Alabama to western Maryland. Outlying populations of the species may be found in northwestern Florida, west Texas, and west-central Oklahoma. It is naturalized east to the Appalachian Mountains from South Carolina north to Pennsylvania, New York, and New England *(11)*. Honeylocust attains its maximum development in the valleys of small streams in southern Indiana and Illinois.

Honeylocust, especially the thornless form, is widely cultivated as an ornamental and shade tree in all countries having a temperate climate.

Climate

In the western portion of its range honeylocust grows in a subhumid climate while in the middle and eastern portions the climate is humid. Normal annual precipitation varies from about 510 mm (20 in) in South Dakota and Texas to more than 1520 mm (60 in) in southern Louisiana, Mississippi, and Alabama. Average annual snowfall varies from none to 102 cm (40 in). Length of the growing season varies from about 150 days in the north and northeast to more than 300 days in the southern extremities of the range.

Honeylocust is tolerant of low temperatures and in the north it is hardy at -29° to -34° C (-20° to -30° F) *(10)*. Northern races harden-off and become dormant relatively early, while growth of southern races continues later into the year. Southern races are subject to frost damage when planted in the north *(7)*. Honeylocust also may suffer frost damage or dieback because of its indefinite or indeterminate annual growth pattern *(4)*. Twigs may continue to elongate until stopped by cold, whereupon the tender terminal internodes are killed by the first frosts. New growth in the spring then comes from the lower lateral buds.

Soils and Topography

Honeylocust is found most commonly on soils in the orders Alfisols, Inceptisols, and Mollisols that originate from limestone or the rich alluvial floodplains of major rivers and streams. Growth is poor on gravelly or heavy clay soils and honeylocust often fails on shallow soils. Although ample soil moisture is necessary for best growth, the species is very resistant to drought. Because of this, it is a valuable species for shelterbelt planting in the Great Plains.

On 20 drought-resistant species of seedlings tested, honeylocust ranked third in alkali tolerance *(7)*. The species is also tolerant of acid soils *(26)*, but best development is usually on soils having a pH between 6.0 and 8.0. From tests incorporating artificially salinized soils, young honeylocusts were found to be tolerant of soil salinity *(13)*. Seed germination was little influenced by as much as 0.20 percent of sodium chloride in the dry weight of soil *(2)*. Salt tolerance has particular economic importance in the North where runoff from highway de-icing salts can damage plantings, and also where plantings are desired on saline soils in arid states. Whether honeylocust can tolerate the cumulative effects of salinity over a period of years is still unknown.

Typically, honeylocust is a bottom land species, most commonly found only on moist fertile soils near streams or lakes. Although it is not common anywhere in the Mississippi River Delta, it frequently grows on low clay ridges and flats in first bottoms and on the secondary flood plains along the Missouri River tributaries in Nebraska.

Over its range honeylocust grows naturally below a maximum elevation of 610 to 760 m (2,000 to 2,500 ft), although the general upper elevational limit for the species is reported as 1520 m (5,000 ft). A 20-year-old plantation growing at 2100 m (6,900 ft) in

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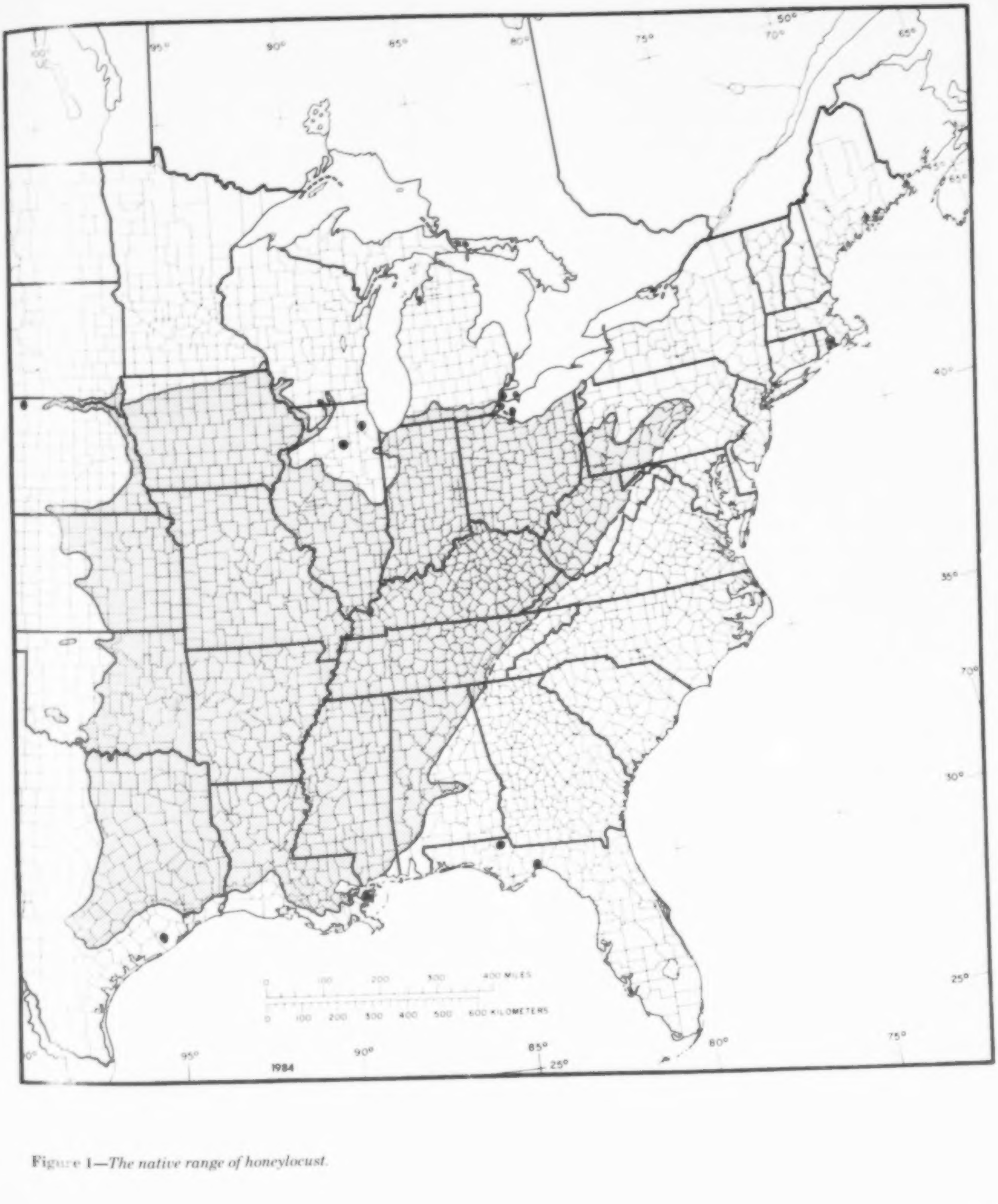
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Figure 1—*The native range of honeylocust.*

Colorado had "good" survival, but trees averaged only 2.4 m (8 ft) in height *(7)*.

Associated Forest Cover

Throughout its range, honeylocust generally occurs only as a minor component of natural forest stands. It is included in four forest cover types in the United States *(19)*. It is an associated species on lowland sites in Bur Oak (Society of American Foresters Type 42), especially in the more southerly portions of the type range, and in Willow Oak–Water Oak–Diamondleaf Oak (Type 88). It is a minor associate in Sweetgum–Willow Oak (Type 92) and Sugarberry–American Elm–Green Ash (Type 93). Mesophytic species commonly associated with honeylocust include red maple *(Acer rubrum)*, persimmon *(Diospyros virginiana)*, blackgum *(Nyssa sylvatica)*, pecan *(Carya illinoensis)*, boxelder *(Acer negundo)*, Kentucky coffeetree *(Gymnocladus dioicus)*, black walnut *(Juglans nigra)*, oaks (*Quercus* spp.), elms (*Ulmus* spp.), ashes (*Fraxinus* spp.), and hickories (*Carya* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowering occurs in late spring, the average date being about May 10 in the southern limit of the range and June 25 in the north *(7)*. Honeylocust leaves are nearly full grown when the flowers are produced, which is usually late enough in the year for the seed crop to escape frost damage.

The species is polygamo-dioecious; flowers are borne in axillary, dense, green racemes *(24)*. Racemes of staminate flowers are 5 to 13 cm (2 to 5 in) long, pubescent, and often clustered. The calyx is campanulate, with five elliptic-lanceolate lobes; there are four to five petals, erect, oval, and longer than the calyx lobes; and up to 10 stamens, inserted on the calyx tube. The pistil is rudimentary or absent in the staminate flowers. Pistillate racemes are 5 to 8 cm (2 to 3 in) long, slender, with few flowers, and usually solitary. The pistils are tomentose, the ovary nearly sessile, and the style short; there may be two ovules or many. The stamens are much smaller and abortive in pistillate flowers.

Seeds, borne in long (15 to 41 cm, 6 to 16 in), flat, indehiscent, and often twisted pods, ripen about mid-September in the southern portion of the range and around mid-October in the north. Soon after fruits mature they begin falling and dissemination often continues into late winter.

Seed Production and Dissemination—Honeylocust begins bearing seed at about 10 years of age, optimum production occurring between 25 and 75 years. Trees continue to bear fruit up to about 100 years of age *(7)*. They generally bear fruit each year and produce abundant seed crops every year or two.

Honeylocust seeds, like those of many leguminous species, have impermeable coats and thus remain viable for long periods of time. Under natural conditions, individual seeds become permeable at different periods following maturation so that any one crop is capable of producing seedlings over a period of several years.

The seeding range or natural dispersal of honeylocust seeds is not extensive. The pods, however, are readily eaten by cattle, whereby seeds are scattered in the feces. Undoubtedly seeds are also disseminated by birds and other mammals that feed on the fruit. Cleaned seeds average about 6,170/kg (2,800/lb), with a commercial purity of 95 percent and a soundness of 98 percent *(24)*. Viability can be retained for several years when seeds are stored in sealed containers at 0° to 7° C (32° to 45° F) *(3)*.

Seedling Development—Germination is thought to be enhanced when seeds are eaten and passed undigested by birds and mammals *(7)*. Passage through the digestive system apparently softens the impermeable seedcoat. Enhanced germination can also be achieved by mechanically scarifying the seeds or soaking them in concentrated sulfuric acid or hot water (88° C, 190° F) for 1 to 2 hours. When hot water is used the water and seeds should be allowed to cool to room temperature or until seeds swell *(3)*. Treated seeds should be sown promptly and not stored. Germination is epigeal.

Honeylocust seedlings show a growth pattern characteristic of deciduous hardwoods with sympodial growth. Persistent terminal buds are not formed and the shoot tip often dies and falls off *(5)*.

Nursery-grown seedlings from pretreated seeds attain suitable size—30 cm (12 in) or more in height—for field planting in 1 year *(3)*. In southern Michigan, first-year seedlings grown in pots reached a height of 37 cm (14.6 in) by September 21, just before leaf abscission *(5)*. The average root-to-shoot ratio was 2 to 3. Stem growth was slow in the spring but rapid in early summer and fall. Only 60 percent of the height growth was attained by mid-July. In an additional study in southern Michigan, nursery seedlings grown 3 years in pots and nearly two growing seasons outplanted in the field averaged 22 mm (0.9 in) in trunk diameter *(16)* by early autumn. The following year trunk diameter increased 4 mm (0.15 in).

Dormant nursery-grown seedlings can be stored, barerooted, at about 0° C (32° F) for several weeks before outplanting with no appreciable loss in survival rate *(15)*.

Vegetative Reproduction—Honeylocust coppices freely. Propagation, particularly of high quality clonal stock, can be achieved by grafting, budding, and cuttings from hardwood, softwood, and roots *(7)*. Root cuttings appear to be the best method of reproducing desirable strains in large quantities at reasonable cost. At times other species or varieties are grafted onto the rootstock of honeylocust *(24)*.

Honeylocust thorn production usually diminishes gradually and finally ceases in the upper and outer crown growth as the tree ages. Thorns may still be produced on the lower trunk and on lower-trunk and limb sprouts. Typical trees, 10 years old or more, show a definite thornless region in the upper and outer shoot growth. When hardwood cuttings for propagation are taken from this thornless area, the scions generally remain thornless *(6)*. Tree breeders can control the sex of scions from honeylocust by selecting unisexual budwood when taking cuttings. Certain branches bear only one type of flower, and trees from cuttings from those branches will bear only that type *(14)*.

Sapling and Pole Stages to Maturity

Growth and Yield—In natural stands, honeylocust (fig. 2) attains a height of 21 to 24 m (70 to 80 ft) and a d.b.h. of 61 to 91 cm (24 to 36 in). On the best sites, trees may be 43 m (140 ft) in height and 152 to 183 cm (60 to 72 in) in d.b.h. On poor sites trees are stunted, wide-branched, and often covered with thorns. In eastern Nebraska, 18- to 35-year-old honeylocust in plantations grew an average of 4.6 cm (1.8 in) in diameter each 10 years.

The average height growth of honeylocust planted in shelterbelts from North Dakota to Texas was 49 cm (19.2 in) per year during the first 7 years *(7)*. This was a slower height growth than for plains cottonwood *(Populus deltoides* var. *occidentalis)* and Siberian elm *(Ulmus pumila)* but faster than that of American elm *(U. americana)*, green ash *(Fraxinus pennsylvanica)*, or hackberry *(Celtis laevigata)*, all of which were frequently planted on the same shelterbelt projects. Under favorable conditions the annual diameter growth of young honeylocust is from 8 to 13 mm (0.33 to 0.50 in) *(22)*. The species is an excellent tree for windbreaks.

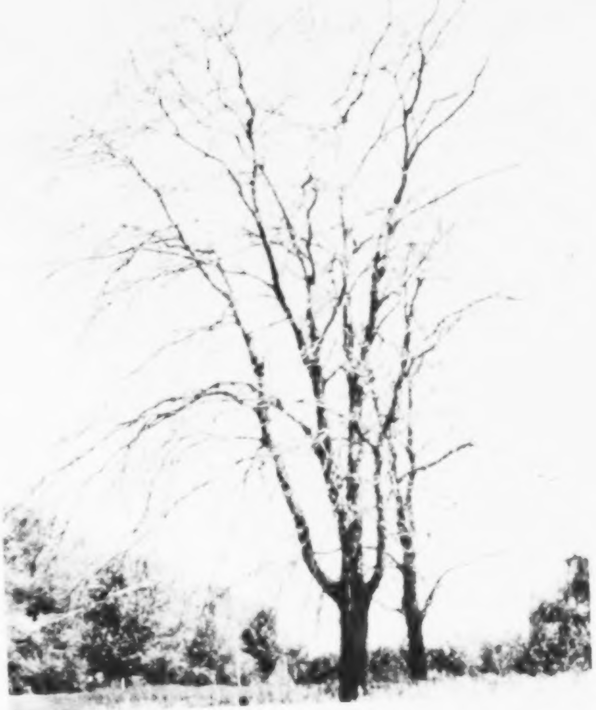

Figure 2—*A mature honeylocust in spring (Courtesy James W. Hanover)*

Rooting Habit—Honeylocust is deep rooted with a widely spreading and profusely branched root system and a strong taproot. Deep soils are penetrated as far as 3 to 6 m (10 to 20 ft). The root system is responsive to environmental conditions. For example, in a Missouri study, 4- to 6-year-old saplings on upland clay soil produced root systems that were about twice as long, with laterals covering twice the area, as those of older trees growing in lowland alluvial soil where the water table was higher *(7)*. The generalized, well-developed root system enables this species to grow on both upland and lowland sites.

Reaction to Competition—Honeylocust is classed as intolerant of shade, and reproduction becomes established only beneath openings in the forest canopy *(5)*. Both top and root growth are retarded where young trees are subjected to shade; therefore, for survival and optimum development, honeylocust must maintain a dominant position in the forest community. Lower limbs of forest-grown trees die when they are excessively shaded from the sides, and the dead limbs often are retained for some time.

Honeylocust is occasionally a pioneer on midwest strip-mine spoil banks. It is also a pioneer in rocky limestone glades of Tennessee and Kentucky, where it is often succeeded by eastern redcedar (*Juniperus virginiana*). In northern Ohio, honeylocust was found with shellbark hickory (*Carya laciniosa*) and bur oak (*Quercus macrocarpa*) in the elm–ash–soft maple association on areas that formerly were swampy (*7*).

Damaging Agents—With the increased popularity and plantings of honeylocust, particularly the cultivars of thornless varieties, there has been a corresponding increase in the kinds and numbers of attacking insects. Generally, insect attacks are not fatal but they do weaken the tree and retard growth. Honeylocust is a host of a number of leaf feeders and severe infestations can rapidly defoliate trees. A severe and widely distributed defoliator is the mimosa webworm (*Homadaula anisocentra*) (*1*). The search for webworm resistant trees has not been productive (*17*). *Eotetranychus multidigituli*, a spider mite common to the midwest, and other mites feed on honeylocust leaves. Heavy infestations, occurring particularly in hot dry weather, will defoliate a tree. The whitemarked tussock moth (*Orgyia leucostigma*), the honeylocust plant bug (*Diaphnocoris chlorionis*) (*25*), the leaf hopper (*Empoasca pergandei*), and several other species of pod galls, leaf rollers, leaf hoppers, moths, loopers, bagworms, and beetles feed on honeylocust foliage. The walkingstick (*Diapheromera femorata*) is also included among the many defoliators (*21*).

Agrilus difficilis, a flatheaded borer, important west of the Mississippi River, burrows beneath the bark and may eventually girdle the trunk or large limbs (*18*). Several other bark and wood borers attack honeylocust, such as the widely distributed *Xyleborus saxeseni*.

A number of scale insects, such as the European fruit lecanium (*Parthenolecanium corni*), which is widespread and particularly damaging to shade trees, and the cottony maple scale (*Pulvinaria innumerabilis*), injure the bark of honeylocust, especially on small branches, lowering the vitality and growth rate of trees (*18*). Weakened trees become subject to attack and further damage by various species of boring insects and bark beetles.

The twig girdler, *Oncideres cingulata*, prunes small branches and can inflict severe injury on nursery seedlings. Heavy infestations can also severely damage large trees. The larvae of *Amblycerus robiniae*, a bruchid weevil, feed on honeylocust seed (*1*). The female periodical cicada (*Magicicada septendecim*) can damage honeylocust, especially young transplanted trees, by depositing eggs in the twigs.

Honeylocust is subject to few diseases, none of which interfere with its growth, except in isolated situations. The most noteworthy disease is the canker *Thyronectria austro-americana*, which can be fatal. Spiculosa cankers cause loss in merchantable wood volume or cull. Honeylocust is subject to several heart-rot and wood-decay fungi from species of *Fomes* and *Polyporus*.

Few leaf diseases attack honeylocust, and none mar the tree. The most widely distributed is tarry leaf spot caused by *Linospora gleditsiae* (*9*). In the seedling stage honeylocust is susceptible to cotton root rot (*Phymatotrichum omnivorum*), which is sometimes fatal (*7*). In shelterbelt planting tests in Oklahoma and Texas it was ranked as highly susceptible to certain *Phymatotrichum* root rots (*27*). Two other root diseases, *Ganoderma lucidum* and *G. curtisii*, can cause extensive root rot and tree fatality. The incidence of these root rots is not high.

In the southeast Texas area honeylocust was visibly damaged but not killed by air pollution, presumed to be mainly sulfur dioxide. In Illinois the species was ranked as highly resistant to ice damage and in Tennessee it was rated about average in resistance to flooding damage (*9*). It also appears to be resistant to salt spray when planted near the coast. Honeylocust is considered to be windfirm, but heavy limb breakage from wind was reported in Kansas. Because of its relatively thin bark it is easily damaged by fire (*7*). Rabbits sometimes inflict damage by gnawing the bark from young trees during the winter.

Special Uses

Honeylocust fruits are readily eaten by cattle and hogs. The beans of some cultivars contain as much as 12 to 13 percent protein, and the pods contain up to 42 percent carbohydrates (*12,20*). Livestock also eat the young vegetative growth and both the fruit and plants are eaten by snowshoe hares and cottontails. Fruits are also eaten by gray squirrels, fox squirrels, white-tailed deer, bobwhite, starlings, crows, and opossum (*7,8*). Honeylocust is a source of honey during the short flowering period in spring.

Both the common honeylocust and its thornless varieties are planted for erosion control and for wind breaks; the thornless varieties are widely planted as shade and ornamental trees. In many urban areas thornless honeylocust has been planted as a replacement for the American elm (*26*).

The wood of honeylocust possesses many desirable qualities but is little used because of its scarcity (*23*).

The sapwood is generally wide and yellowish in contrast to the reddish-brown heartwood, providing an attractive grain. The wood is dense, very heavy, very hard, strong in bending, stiff, resistant to shock, and is durable when in contact with soil. It is used locally for fence posts, and also as lumber for pallets, crating, and general construction.

Genetics

Races and Hybrids

The honeylocust has wide genetic variations that have enabled improvement through selection. The northern races show relatively good winter hardiness and southern races bear fruit that is much more nutritious for stock feeding than that found on the trees in the north *(6)*.

A number of horticultural forms have been developed and are widely cultivated, especially for shade and as ornamentals *(24)*. Thornless honeylocust *(Gleditsia triacanthos* var. *inermis* Willd.) is thornless, or nearly so, and slender in habit; bushy honeylocust *(G. triacanthos* var. *elegantissima* [Grosdemange] Rehd.) is unarmed and densely bushy; Bujot honeylocust *(G. triacanthos* var. *bujotii* [Neum] Rehd.) has slender pendulous branches and narrow leaflets; and dwarf honeylocust *(G. triacanthos* var. *nana* [Loud.] A. Henry) is a small compact shrub or tree. Selected cultivars of the thornless forms have been patented. About 60 percent of the seedlings grown from thornless honeylocust seed are thornless *(7)*.

Gleditsia × texana Sarg., the Texas honeylocust, is considered to be a hybrid of *G. aquatica* Marsh. and *G. triacanthos* L. *(24)*. Its range is largely restricted to the Brazos River bottoms in Texas, with additional trees found along the Red River in Louisiana and occasionally along the Mississippi River in Indiana and Mississippi.

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Gordonia lasianthus (L.) Ellis   Loblolly-Bay

Theaceae   Tea family

Charles A. Gresham and Donald J. Lipscomb

Loblolly-bay *(Gordonia lasianthus)*, also called holly-bay, gordonia, and bay, is a small to medium-sized evergreen tree or shrub found in acid, swampy soils of pinelands and bays on the Atlantic and Gulf Coastal Plains. It is slow growing with soft, light-colored, fine-grained wood of little commercial value, although loblolly-bay could be managed as a source of pulpwood. The white showy flowers and shiny foliage make it a desirable ornamental, but it is not easy to cultivate. Deer browse stump sprouts heavily.

Habitat

Native Range

Loblolly-bay (fig. 1) is continuously distributed along the Atlantic and Gulf Coastal Plains from the Albermarle Sound of North Carolina to the Apalachicola River in the Florida Panhandle. Discontinuous populations exist in Florida, the coastal counties of Alabama, and southern Mississippi. In

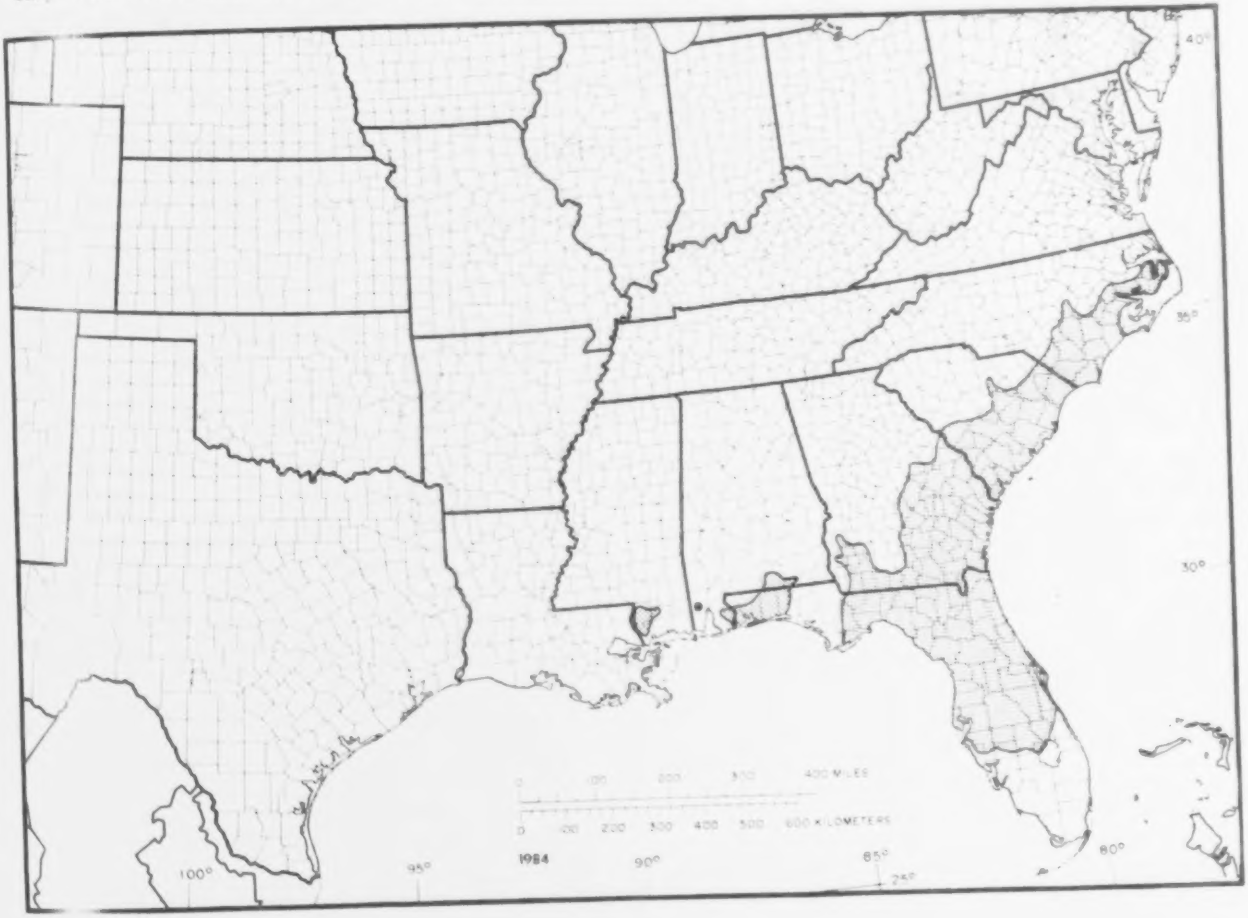

Figure 1—*The native range of loblolly-bay.*

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South Carolina it is commonly found in the lower Coastal Plain, but in the middle and upper Coastal Plain it is restricted to specific sites.

Climate

The climate over the range of loblolly-bay is characterized by mild winters and warm summers. Air temperature data, compiled from a weather atlas *(8)*, are as follows:

	Northern extreme	Southern extreme
Temperature:		
Annual daily average	16° C (60° F)	21° C (70° F)
Normal daily min., January	3° C (37° F)	11° C (52° F)
Normal daily max., July	31° C (87° F)	32° C (90° F)
Normal daily range	11° C (52° F)	10° C (50° F)
Days with daily max. above 32° C (90° F)	20	120
Days with daily min. below 0° C (32° F)	50	3
Mean frost-free days	230	320

The average annual precipitation within the range of loblolly-bay is 1630 mm (64 in) in Florida, declining to 1120 mm (44 in) in North Carolina, and is fairly evenly distributed throughout the year.

Approximately 53 percent of the annual precipitation occurs during the months of June, July, August, September, and October. Annually there are from 110 to 120 days with only a trace of rainfall.

Soils and Topography

In North and South Carolina, loblolly-bay is apparently very soil-specific even though it is found on several soil series. It grows on certain Spodosols, Inceptisols, Ultisols, and Histosols and to a lesser degree on Entisols and Mollisols *(7)*. Soil profiles of a loblolly-bay site in South Carolina have the following general characteristics:

A_1—0 to 25 cm (0 to 10 in) black to dark gray, fine sand, loamy fine sand or loamy sand, very strongly or extremely acid,

A_2—25 to 38 cm (10 to 15 in) black or gray, sand, loamy fine sand or sandy loam, very strongly or extremely acid (often there is no A_2),

B—38 to 51 to 127 cm (15 to 20 to 50 in) gray or brown, sand to sandy loam, very strongly acid (often not present),

C—51 to 127 to 175 cm (20 to 50 to 69 in) gray or brown, sand, fine sand or loamy fine sand, strongly to very strongly acid.

Loblolly-bay grows in flat woodlands or shallow depressions with little or no slope, slow runoff, rapid permeability, and poor to very poor drainage. In South Carolina the soils are usually of sandy coastal plain or marine origin, except for the organic soils. The water table is at or near the soil surface for 6 to 9 months of the year.

In South Carolina's lower Coastal Plain, loblolly-bay is found in wet flats and in bays, typically the Carolina Bays *(11)*. In the upper and middle Coastal Plain, it is found mainly along the edges of Carolina Bays and is widely dispersed in wet, flat woodlands on certain soil types.

Associated Forest Cover

Loblolly-bay is found in five forest cover types *(2)* within the Atlantic Coastal Plain *(9,10,11)*. Pondcypress (Society of American Foresters Type 100) is found in certain Carolina Bays with ponded water. Loblolly-bay is not found in the bay interior with pondcypress *(Taxodium distichum* var. *nutans)*, probably because of the high water table; rather it is found along better drained margins. Here it is growing with loblolly pine *(Pinus taeda)* and redbay *(Persea borbonia* var. *borbonia)* in the overstory and fetterbush *(Lyonia lucida)*, inkberry *(Ilex glabra)*, and greenbrier *(Smilax* spp.) in the understory.

Loblolly-bay is a minor component of Loblolly Pine–Hardwood (Type 82) but cannot be found consistently. In the middle Coastal Plain of South Carolina, loblolly-bay is found with loblolly pine, water oak *(Quercus nigra)*, sweetgum *(Liquidambar styraciflua)*, American holly *(Ilex opaca)*, redbay, longleaf pine *(Pinus palustris)*, and yellow-poplar *(Liriodendron tulipifera)*. Loblolly-bay is found only in the wetter areas of this forest cover type.

Loblolly-bay is a minor component of Atlantic White-Cedar (Type 97), along with pond pine *(Pinus serotina)*, swamp cyrilla *(Cyrilla racemiflora)*, redbay, and sweetbay *(Magnolia virginiana)*.

Pond Pine (Type 98) is the typical vegetation of wet flats and some Carolina Bays in South Carolina. Loblolly-bay, pond pine, sweetbay, and redbay are the tree species present, and they rarely form a closed canopy. The thick, shrub layer is composed of fetterbush, greenbrier vines, inkberry, and loblolly-bay.

Sweetbay–Swamp Tupelo–Redbay (Type 104) is the "broadleaf evergreen forest" of the lower Coastal Plain of North and South Carolina. Loblolly-bay is a minor component in the overstory along with red maple *(Acer rubrum)*, black tupelo *(Nyssa sylvatica* var. *sylvatica)*, sweetgum, and water oak.

Life History

The information of this section is based on measurements and observations made in the northern Coastal Plain of South Carolina.

Reproduction and Early Growth

Flowering and Fruiting—Flowers are perfect. Flower bud formation is visible by the time new leaves fully expand. The peduncle expands rapidly and the young bud slowly enlarges until it opens. Flower buds at the top of the tree open first. Flowers are first seen from the last week in June to the first week of July and may be seen until mid-August. Flowers remain open for 1 or 2 days and are pollinated by bumble bees, thrips, flies, and hummingbirds. After the second day the sepals and petals fall, leaving the ovary at the end of the peduncle.

Seed Production and Dissemination—As the ovaries develop they gradually turn brown and five sutures develop. Mature, open capsules are first seen during September or October, and all of the capsules open by the middle of December. Seeds are shaken out of the capsules by the wind and empty capsules remain attached until peduncle and capsule abscision, which first occurs about the last of December and continues through the winter.

Seedfall starts in October, peaks in December, and continues until the first of March. Loblolly-bay seeds are light (264,550 to 332,895/kg or 120,000 to 151,000/lb) and winged. Results from one study indicated that approximately 99 percent of the seeds produced fall within two tree heights of the source tree. This study also indicated that this distribution of seedfall is concentrated near the source tree, 60 percent of the seeds falling within a distance equal to one-half of the tree height, and 94 percent of the seeds falling within a distance equal to the tree height. Seedfall rates during a 2-year study varied from 2,645 to 272,920/ha (1,070 to 110,449/acre).

Seedling Development—Seed germination in petri dishes in sunlight is high: 70 to 80 percent within 10 days. In a greenhouse heated at 13° to 16° C (55° to 60° F), similar germination percentages were obtained but up to 24 days were required. Germination is epigeal. Very few seedlings have been observed in the field and most of those seen apparently do not live past the first season. Loblolly-bay seedlings seem to require relatively open conditions and exposed soil for establishment. Older seedlings have only been observed where the mineral soil has been disturbed such as in recently plowed fire lines.

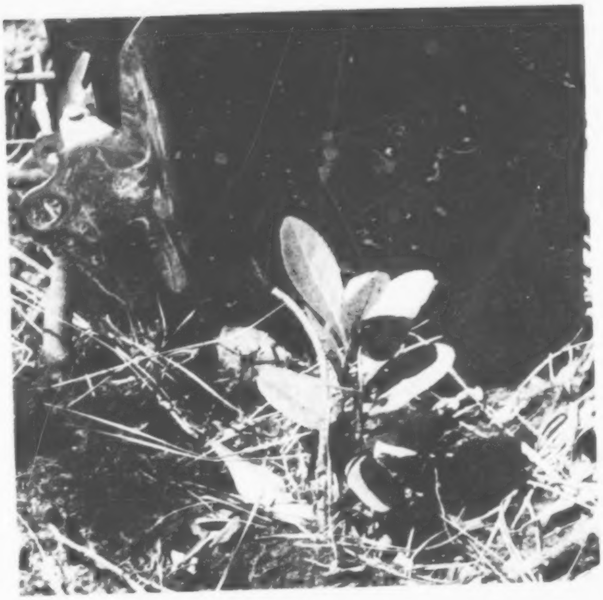

Figure 2—*A loblolly-bay seedling.*

Initial growth of the seedlings (fig. 2) is slow. Field observations indicated that by the end of the third growing season the seedlings were about 10 to 15 cm (4 to 6 in) tall and by the eighth growing season they were only 30 to 40 cm (12 to 16 in) high.

Vegetative Reproduction—Vegetative propagation of first-year shoots in a peat and sand medium under mist is commonly used by horticulturists *(1)*. In the field, vegetative regeneration appears to be more common than regeneration from seed. Stump sprouts may grow as much as 1 m (3 ft) the first year after the tree is cut. These stump sprouts appear to be very attractive to deer and heavy browsing has been noticed.

Numerous root-collar sprouts are produced when the trees are killed by fire *(9)* or if the root system is mechanically damaged by a logging or disking operation.

Sapling and Pole Stages to Maturity

Growth and Yield—Early tree growth (ages 5 to 15 years) (fig. 3) is relatively rapid. Height growth for the first 15 years averages 0.6 m/yr (2.0 ft/yr), with a 10-year-old tree averaging 6.5 m (21.3 ft) in height. These figures do not compare with the seedling's growth figures because growth and yield meas-

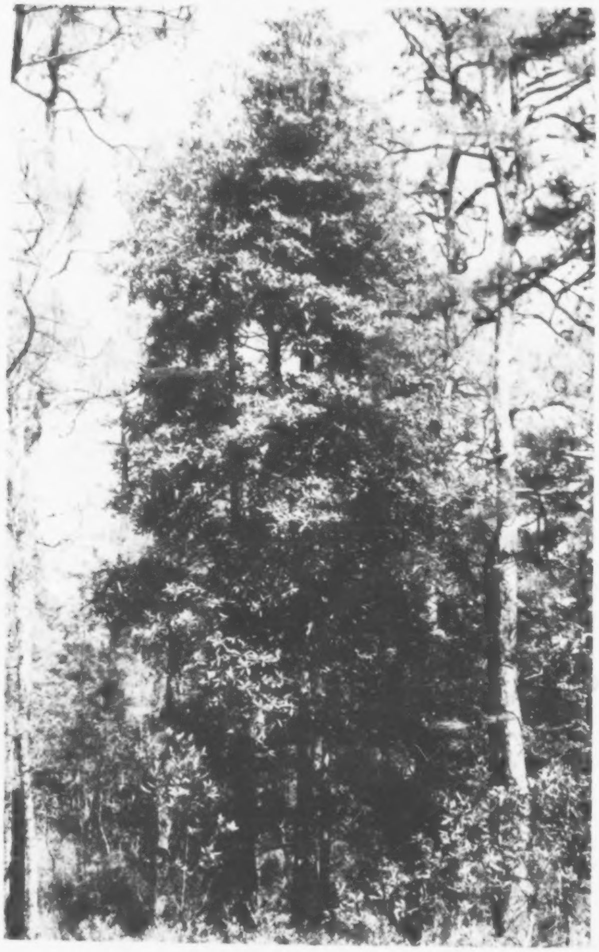

Figure 3—*Loblolly-bay tree in Georgetown County, SC, at age 25 years.*

urements were made on stems that were most probably sprouts. Early diameter growth at breast height is about 0.4 cm/yr (0.2 in/yr), a 10-year-old tree being about 5.1 to 6.1 cm (2.0 to 2.4 in) in d.b.h.

Rooting Habit—The root system of loblolly-bay appears to reflect its strong tendency to reproduce by sprouting. A number of specimens examined had a large primary lateral root with secondary roots branching downward.

Reaction to Competition—Loblolly-bay is classed as tolerant of shade. In bays and wet flats, where the tree cover is relatively light, loblolly-bay is a strong competitor. It generally increases in height faster than the pines on the adjacent upland. However, if loblolly-bay is overtopped, older trees will lose their characteristic conical shape and the crown will break up.

Damaging Agents—Only two symptoms of insects or pathogens have been observed locally. Neither causal agent was identified. An ooze was noticed in a wound at the base of a mature tree, but otherwise the tree appeared healthy. An unknown grazing insect consumed all but the leaf veins of the late-season flush of leaves during August. Another noticeable sensitivity is to fire. The thin bark and shallow root system of loblolly-bay probably contribute to its low fire tolerance.

Special Uses

Loblolly-bay has long been used by horticulturists in landscaping *(1)*. Most research on loblolly-bay has been done by horticulturists interested in propagating it. In the Southeast, loblolly-bay is considered a handsome and hardy tree valued for its glossy dark-green leaves and abundant white flowers. Its wood has been used in cabinetmaking and its bark as a tanning agent *(5)*.

Because of its ability to grow in wet bogs and flats where loblolly pine does poorly, loblolly-bay silviculture may offer a management alternative for such areas.

Laboratory papermaking tests conducted recently and other results reported in the literature *(3,4)* indicate that the pulp yield from loblolly-bay was acceptable (52 percent), the bulk of the paper was low (1.46 cm/g or 2.53 in/oz), and the strength acceptable. One laboratory test indicated a breaking length of 11,525 m (37,812 ft), a tensile strength of 10.2 kg/15 mm (38.1 lb/in), and a count of 836 folds using the Massachusetts Institute of Technology paper folding tester (1 kg or 2.2 lb). Although further testing needs to be done, these tests do not indicate any problems in making kraft paper from loblolly-bay pulp. Pulp mills in the lower Coastal Plain of South Carolina include loblolly-bay in their hardwood pulp.

Genetics

Because loblolly-bay is the only native tree in the genus *(6)*, there are no hybrids. No information could be found concerning the genetics of loblolly-bay.

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Grevillea robusta A. Cunn. Silk-Oak

Proteaceae Protea family

Roger G. Skolmen

Silk-oak *(Grevillea robusta)*, also often called silver-oak, is a medium to large tree commonly planted as an ornamental in many warm-temperate and semitropical climates. It has been established as a forest tree in some countries and shows promise as a fast-growing timber tree.

Habitat

Native Range

Silk-oak is native to coastal eastern Australia from the Clarence River, New South Wales, to Maryborough, Queensland, and is now naturalized in Hawaii and southern Florida *(3,16)*. It was introduced into Hawaii about 1880 and is found on all islands where it reproduces prolifically in certain leeward grassland locations. Although a nongregarious tree in its native habitat, it grows well in pure plantations in Hawaii *(18)*. It is common as an ornamental in Hawaii, Florida, California, and Puerto Rico *(5)*. Because of its prolific reproduction, it has been classed a noxious weed on ranchland in Hawaii *(9)*. In the tropical highlands of India, where it has also been extensively planted, it is often an undesirable escapee from cultivation *(13)*.

Climate

In Hawaii, silk-oak has been planted extensively in both wet and dry locations on all islands from near sea level to more than 900 m (3,000 ft) elevation *(9)*. The mean temperature ranges from 10° to 26° C (50° to 78° F) within this elevational range, with extremes of 4° and 35° C (40° and 95° F). Silk-oak, for many years, was thought to be best suited for planting in arid areas because of its success as a seedling and sapling in such areas. Later it became apparent that frequent severe moisture stress in the dry areas (less than 760 mm [30 in] annual rainfall) caused disease susceptibility resulting in dieback as the trees became older. Natural reproduction, however, was sometimes excellent in these dry locations. The largest silk-oak trees in Hawaii grow in 3050 mm (120 in) winter maximum or evenly distributed annual rainfall at 610 m (2,000 ft) elevation, but the most prolific natural reproduction coupled with excellent growth occurs in 1780 to 2400 mm (70 to 95 in) evenly distributed annual rainfall at 460 to 670 m (1,500 to 2,000 ft) elevation. Elsewhere than Hawaii, silk-oak is reported to be capable of withstanding occasional light frosts but must be considered frost-tender *(16)*. It is also reported elsewhere to be fairly hardy to drought but tends to die back on droughty sites at 15 to 20 years of age *(2)*.

Soils and Topography

Silk-oak is tolerant of a wide range of soils if they are well drained *(16)*. It will grow on neutral to strongly acid soils but does best on those that are slightly acid *(2,12)*. In Hawaii, good growth is achieved on soils of a wide range of orders. Silk-oak grows well on Histosols, Inceptisols, and Ultisols. The majority of the best stands are on Dystrandepts and Tropofolists developed on gentle to moderate slopes of basalt lava rock or ash.

Associated Forest Cover

Where planted in pure stands in Hawaii, silk-oak maintains its purity with little woody competition. In naturalized stands, it grows in association with many other tree species including the native koa *(Acacia koa)*, 'ohi 'a *(Metrosideros collina)*, and introduced species such as tropical ash *(Fraxinus uhdei)*, jacaranda *(Jacaranda mimosifolia)*, molucca albizzia *(Albizia falcataria)*, black-wattle *(Acacia decurrens)*, Christmas-berry *(Schinus terebinthifolius)*, and guava *(Psidium guajava)*.

Life History

Reproduction and Early Growth

Although it is most commonly grown in nurseries and planted, silk-oak regenerates naturally at the edges of plantations, in openings within plantations, and under open stands of other species. It does not regenerate directly underneath itself either in closed stands or under open-grown trees. Natural regeneration is reported from India, Tanzania, and Queensland, Australia (at the edges of plantations), as well as from Hawaii *(6,9,11,12,14,16,18)*.

Flowering and Fruiting—In Hawaii, silk-oak flowers from March through October, with the peak of flowering usually in June. The perfect yellowish-

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Figure 1—*Silk-oak flowers and leaves.*

orange, showy flowers are borne on 8- to 18-cm (3- to 7-in) long racemes that occur in panicles of one to several branches *(3)*. Trees usually begin to flower at about 10 years (fig. 1). The fruit, a podlike follicle, 20 mm (0.8 in) in diameter, is slightly flattened and has a long-curved style. The hard dark-brown to black follicle splits open in late fall to release the one or two seeds it contains but remains on the tree up to 1 year after opening. Trees near San Jose in California have been observed to flower, fruit, and seed at times similar to those in Hawaii.

Seed Production and Dissemination—Silk-oak is a prolific seeder. Seeds are about 10 mm (0.4 in) long, flattened, and surrounded by a membranous wing. There are reported to be 64,000 to 154,000 seeds per kilogram (29,000 to 70,000/lb). Because of their relatively large wing, the lightweight seeds are widely disseminated by wind. Possibly because seedfall coincides with the onset of winter rains in dry leeward rangeland in Hawaii, regeneration is most prolific on these sites.

The seeds, if kept at 10 percent or less moisture content, can be stored for as long as 2 years at –7° to 3° C (20° to 38° F) with little loss in germinability. Germination of fresh, unstratified seeds requires about 20 days. Stratification at 3° C (38° F) for 30 days or a 48-hour water soak, substantially increases germinative capacity of seeds that have been stored *(19)*.

Seedling Development—Germination is epigeal. Seedlings are grown in flats or containers in nurseries. Methods vary among the countries where silk-oak is grown. In some countries 4- to 6-week-old wildings are lifted and potted and later replanted *(2)*. Elsewhere plants are grown to 45-cm (18-in) heights in large baskets so that they can compete when outplanted *(12)*. In Hawaii, seedlings in individual containers can be grown to a plantable size of 20 cm (8 in) height and 4 mm (0.16 in) caliper in 12 to 14 weeks.

Vegetative Reproduction—Silk-oak coppices when cut. After being damaged by fire, a 5-year-old stand in Karnataka State, India, was cut. One year later, 93 percent of the stumps had coppiced. After 2 years 72 percent of the stumps still retained the coppice shoots, which by then averaged 4 m (13 ft) in height *(1)*. As far as is known, vegetative propagation has not been practiced with the species.

Sapling and Pole Stages to Maturity

Growth and Yield—In Hawaii, the tree usually produces a straight, erect stem even when open-grown *(15)*. Where subjected to drought stress sufficiently severe to cause dieback, it forms forks and multiple leaders. On good sites (500 m; 1,600 ft altitude; 2030 mm; 80 in annual rainfall), dominant trees planted at spacing of 3 by 3 m (10 by 10 ft) can be expected to be 8 to 9 m (25 to 30 ft) tall in 5 years, 15 m (48 ft) in 10 years, and 20 m (65 ft) or more in 20 years *(11)*. Mean annual increment of dominants on 21 different sites in Uganda, for trees 2 to 20 years in age, ranged from 1.3 to 3.3 cm (0.5 to 1.3 in) in diameter and from 0.5 to 3.4 m (1.7 to 11.2 ft) in height *(4)*. This indicates that the tree is fast growing as a sapling and pole.

Many plots have been measured in 32- to 48-year-old silk-oak plantations in Hawaii *(11)*. All the plantations had been planted at 3 by 3 m (10 by 10 ft) and left untended since planting. Average d.b.h. of dominant and codominant trees at 44 years in four of the plots was 46 cm (18 in), and the average total height was 32 m (105 ft). The most outstanding stand, at 36 years, yielded a mean annual increment of 17.5 m^3/ha (1,250 fbm/acre) *(11)* (fig. 2). Typically, merchantable trees in these untended stands were 36 to 46 cm (14 to 18 in) d.b.h. with 9 to 11 m (30 to 36 ft) of branch-free stem.

In India, trees reach 50 cm (20 in) diameter in 30 years when grown at an initial spacing of 3 by 4 m (10 by 13 ft) and thinned once at about 5 years, and again later if needed to maintain growth rate. Such stands yield about 140 m^3/ha (2,000 ft^3/acre) with another 70 m^3/ha (1,000 ft^3/acre) from thinnings *(13)*.

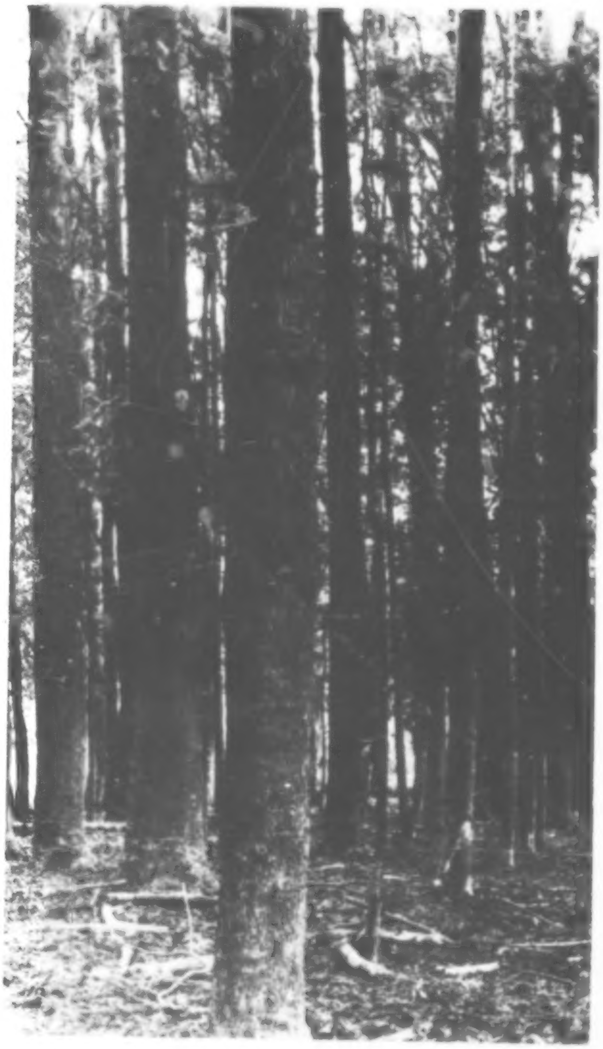

Figure 2—*Silk-oak stand at Kapapala Ranch, Island of Hawaii, which yielded 1470 m³/ha (105,000 fbm/acre) when harvested at age 36.*

One 14-year-old plantation had a mean diameter of 27 cm (11 in) and height of 19 m (61 ft) and yielded 217 m³/ha (3,100 ft³/acre) *(13)*. Another author in India suggests that silk-oak at 10 to 15 years and 1,000 stems per hectare (370/acre) yields 10 to 12 m³/ha (143 to 172 ft³/acre) *(10)*. In the western Himalayas, 6-year-old silk-oak had outgrown 45 other species, including such fast growers as *Eucalyptus globulus*, *Populus* × *euroamericana*, and *Albizia lebbek (17)*.

Rooting Habit—Silk-oak does not develop a strong taproot and roots shallowly on sites that lack moisture stress *(16)*. On droughty sites it roots throughout the soil profile to depths of about 2 m (6 ft).

Reaction to Competition—Silk-oak is classed as very intolerant of shade. In Australia, seedlings do not survive beneath closed pure stands of the species because of some substance toxic to them that is produced by or associated with roots of the trees *(18)*. This substance is specific to silk-oak seedlings, causing rapid chlorosis, blackening, and death of seedlings soon after they emerge and begin to grow. Consequently, the tree is nongregarious in its natural habitat. The toxic substance has not been investigated in Hawaii, but it has been observed that reproduction is lacking within dense stands or directly beneath individual trees.

In Hawaii, silk-oak has been planted in mixture with numerous other species. Two of the species it dominates when in mixture are melaleuca (*Melaleuca quinquenervia*) and horsetail casuarina (*Casuarina equisetifolia*). Three that grow well in mixture with it are Australian toon (*Toona ciliata* var. *australis*), tropical ash, and koa. Three that dominate silk-oak are Norfolk-Island-pine (*Araucaria heterophylla*), saligna eucalyptus (*Eucalyptus saligna*), and robusta eucalyptus (*E. robusta*).

In Brazil, several spacing studies indicated that at 2 years, a spacing of 1 by 3 m (3 by 10 ft) resulted in the best height growth, but at 6 years, 2 by 2 m (6 by 6 ft) was best, with thinning planned at age 10 or 15 (Viega 1958 as cited in *2*). In Brazil, an attempt is made to maintain a basal area of 49 to 61 m²/ha (213 to 265 ft²/acre) throughout the life of the stand. In Hawaii, silk-oak has always been planted at a spacing of 3 by 3 m (10 by 10 ft) and left untended. In Uganda experiments, a number of thinnings were made at various ages, but with little apparent effect on mean annual diameter increment *(4)*.

Damaging Agents—The oleander pit scale, *Asterolecanium pustulans* Cockerell, was so damaging in Puerto Rico that further planting of the species was discouraged *(7)*. *Amphichaeta grevilleae* is a serious leaf spot and defoliating disease in India where it kills young plants *(14)*. Also in India, a serious dieback is caused by a fungus, *Corticium salmonicolor (8)*. No serious primary insects or diseases of the species have been noted in Hawaii, although severe dieback, believed caused by drought, is common on most droughty sites.

Special Uses

Grevillea robusta is a popular ornamental because of its fernlike foliage even in areas where it does not flower abundantly, such as California and Florida north of Miami. In more tropical climates its showy flowers cause it to be widely used.

It has been planted extensively in India and Sri Lanka as shade for tea, and in Hawaii, India, and Brazil to some extent as shade for coffee *(2,12,14,16)*. It is frequently used as a windbreak, although opinions differ as to its wind firmness and branch-shedding tendencies *(2)*. Silk-oak is an important honey tree in India where it is also regarded as a good fuelwood producer *(13)*.

The tree produces an attractively figured, easily worked wood, which was once a leading face veneer in world trade, where it was marketed as "lacewood." The wood contains an allergen that causes dermatitis for many people *(15)*.

Genetics

No studies of the genetics of the species have been reported *(2)*. A test of 11 different genera in Brazil showed 1-year-old silk-oak seedlings to be the most uniform in height growth (Silva and Reichmann 1975 cited in *2*).

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Halesia carolina L. Carolina Silverbell

Styracaceae Storax family

Earl R. Sluder

Carolina silverbell (*Halesia carolina*) is common and reaches its greatest size in the southern Appalachian Mountains where it is called mountain silverbell. This attractive shrub or small tree, also called snowdrop-tree or opossum-wood, grows in moist soils along streams in the understory of hardwood forests. It has a moderate growth rate and lives about 100 years. The wood is soft and close-grained and a favorite wood for crafts. The white bell-shaped flowers and small size make it a desirable tree for landscaping. The seeds are eaten by squirrels and the flowers provide honey for bees.

Habitat

Native Range

Carolina silverbell (fig. 1) grows mostly in the Piedmont and mountains of the Carolinas, eastern Tennessee, Georgia, and Alabama. Its distribution extends beyond this central area, however, in small populations scattered over the southeastern Coastal Plain, western Virginia, West Virginia, southern Ohio, southern Indiana, southern Illinois, Kentucky, Tennessee, central Arkansas, and southeastern Ok-

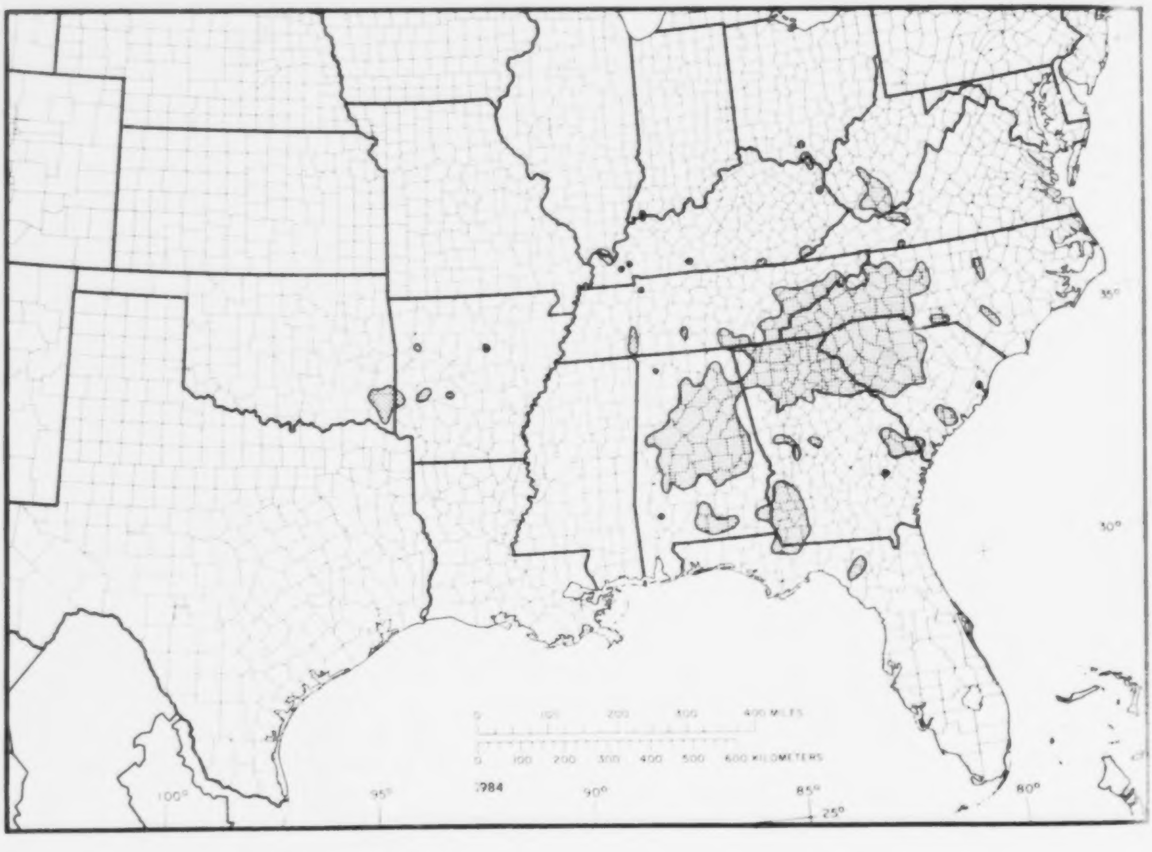

Figure 1—*The native range of Carolina silverbell.*

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lahoma *(6,27,30)*. The species has been successfully cultivated as far north as southern New England, in California, and in Europe *(16,17,30)*.

Climate

The climate over the range of Carolina silverbell is superhumid in the southern Appalachians and humid in the other areas, with temperatures that vary considerably with latitude and elevation. Average annual precipitation varies between 1020 mm and 1140 mm (40 and 45 in) in the northern part of the range to more than 2030 mm (80 in) in the southern Appalachians. Precipitation is well distributed over the year. Average January temperatures range from -1° to 13° C (30° to 55° F) and average July temperatures range from 21° to 27° C (70° to 80° F). The average annual maximum temperatures range from 32° to 41° C (90° to 105° F) and the average minimum from -4° to -21° C (25° to -5° F). The length of the frost-free period ranges from 180 to 280 days.

Soils and Topography

Soils over the range of Carolina silverbell are mostly Ultisols but include sandy Entisols in the Southeast, Inceptisols in the mountains, and Mollisols in southern Illinois *(32)*. The species prefers rich, moist, well-drained, loamy soil that is slightly acid in reaction (pH 5.0 to 6.0). It can tolerate soils more acid than that and may do well in soils with a pH up to 7.0 *(11,23)*.

Carolina silverbell grows mostly along streams, river bluffs, and ravine slopes in the Piedmont and other lowlands and along streams, in coves, and on moist lower slopes in the mountains *(4,8,10,24,28,30)*. It is significant in frequency at elevations between 1370 and 1680 m (4,500 and 5,500 ft) and locally abundant at elevations between 460 and 1370 m (1,500 and 4,500 ft) in the mountains *(10,25)*.

Associated Forest Cover

Sites preferred by Carolina silverbell, the most mesic with the best soils, are those on which a number of hardwoods reach their best development. Consequently, it is found in association with a large number of hardwood species as well as occasionally with conifers.

In Piedmont areas, the species is associated with yellow-poplar *(Liriodendron tulipifera)*, white ash *(Fraxinus americana)*, red maple *(Acer rubrum)*, white oak *(Quercus alba)*, American holly *(Ilex opaca)*, eastern redbud *(Cercis canadensis)*, and bigleaf magnolia *(Magnolia macrophylla)*. In the southern part of its range it occurs with American beech *(Fagus grandifolia)*, southern magnolia *(M. grandiflora)*, American holly, various oaks, cabbage palmetto *(Sabal palmetto)*, Florida maple *(Acer barbatum)*, eastern hophornbeam *(Ostrya virginiana)*, and eastern redbud *(4)*. In the Black Mountains of North Carolina, Carolina silverbell is a significant associate in the northern hardwoods climax association at high elevations and in the cove climax and mesic slope associations at mid-elevations *(10)*. It occurs and may share canopy dominance with eastern hemlock *(Tsuga canadensis)*, yellow buckeye *(Aesculus octandra)*, white basswood *(Tilia heterophylla)*, sugar maple *(Acer saccharum)*, and yellow birch *(Betula alleghaniensis)* in the Great Smoky Mountains and the Joyce Kilmer Memorial Forest *(20,24,25,35)*. Prominent associates of the species in a gorge in the Blue Ridge Mountains of western North Carolina were northern red oak *(Quercus rubra)*, chestnut oak *(Q. prinus)*, sweet birch *(Betula lenta)*, yellow-poplar, flowering dogwood *(Cornus florida)*, and Fraser magnolia *(Magnolia fraseri)*.

Carolina silverbell is associated with the following forest cover types (Society of American Foresters) *(13)*:

23	Eastern Hemlock
24	Eastern Hemlock-Yellow Birch
25	Sugar Maple-Beech-Yellow Birch
26	Sugar Maple-Basswood
27	Sugar Maple
28	Black Cherry-Maple
57	Yellow-Poplar
58	Yellow-Poplar-Eastern Hemlock
59	Yellow-Poplar-White Oak-Northern Red Oak
60	Beech-Sugar Maple
74	Cabbage Palmetto
76	Shortleaf Pine-Oak
82	Loblolly Pine-Hardwood
87	Sweetgum-Yellow-Poplar
91	Swamp Chestnut Oak-Cherrybark Oak

Life History

Reproduction and Early Growth

Flowering and Fruiting—Carolina silverbell (fig. 2) has perfect flowers which appear as the leaves begin to expand in March to May, depending upon location *(8,24,30)*. Each flower has a four-celled ovary, but usually only one cell produces a viable seed *(15,17)*. Larger flower crops are produced annually after the 20th to 25th year *(17)*. The fruit is

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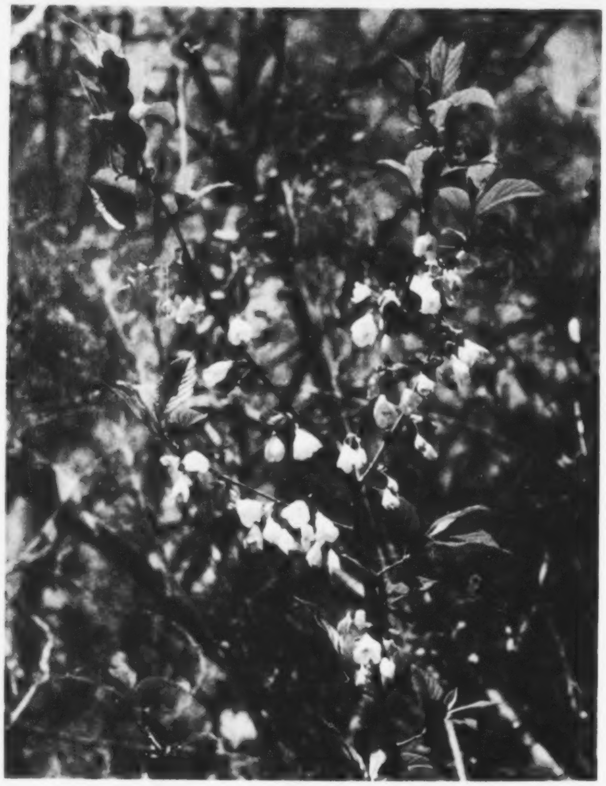

Figure 2—*Foliage and flowers of Carolina silverbell.*

a dry, oblong, four-winged drupe that matures in the fall.

Seed Production and Dissemination—Large seed crops are produced annually by older trees of Carolina silverbell but much of the seed is sterile. The fruits are persistent and dissemination occurs well into the winter. The seeds are dormant to varying degrees at maturity and require special handling to break the dormancy. They require 2 to 3 months of warm, moist storage at 21° to 27° C (70° to 80° F) followed by a similar period of cold stratification at 1° to 5° C (34° to 41° F). Even with this treatment, germination of filled seeds may be 50 percent or lower *(1,15)*. Seeds disseminated in nature or sowed in a nursery without special treatment germinate mostly during the second growing season *(11)*. Fruits to be stored should be kept dry and cold, but no data are available on long-term storage *(5)*.

Seedling Development—Germination of Carolina silverbell seeds is epigeal. Seedlings grow to about 12 cm (5 in) the first 7 weeks. Growth continues at a moderate rate for a few years, then slows considerably *(17)*.

Vegetative Reproduction—Carolina silver bell can easily be propagated by root and greenwood cuttings and by air-layering. Rooting hormones are not necessary for success but may enhance rooting at certain times of the year. For best success, cuttings should be taken after elongation of new growth but before hardening beings. Roots should not be disturbed until the end of the second season. Micropropagation techniques are being developed *(1,3,11,17)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Over most of its range, Carolina silverbell (fig. 3) is an understory shrub or small tree usually reaching heights of 6 to 12 m (20 to 40 ft) with a crown spread of 4.5 to 9 m (15 to 30 ft) and stem diameters of 12 to 27 cm (5 to 11 in). On good sites in the Great Smoky Mountains, how-

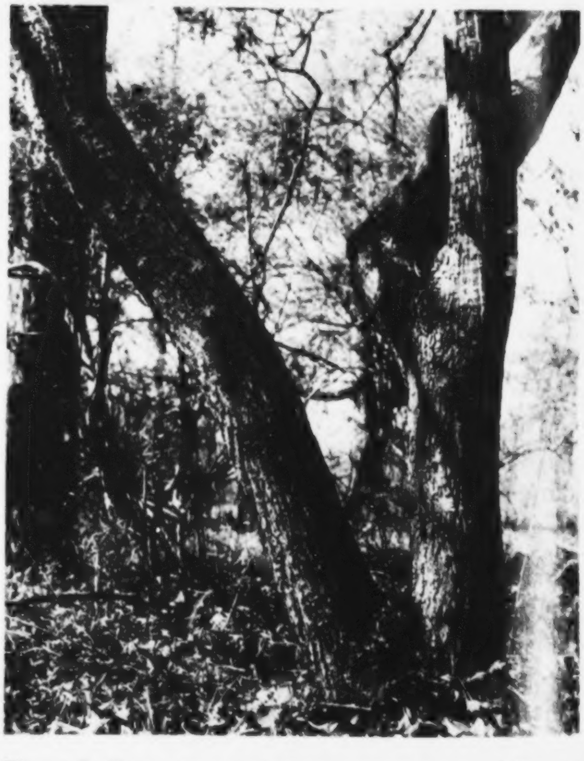

Figure 3—*Two mature stems on a common stump of Carolina silverbell growing on the bank of the Ocmulgee River, Jones County, GA.*

ever, some trees reach 30 m (100 ft) in height and 90 cm (36 in) in d.b.h. Only on cove and north slope sites in the mountains do trees of this species maintain crown positions in the upper canopy and reach large sawtimber size *(8,12,23,24)*. Growth rates of individual trees are moderate to slow, the smaller ones showing 6 to 9 rings per centimeter (15 to 23/in) *(12,17,24)*. No data are available on volumes per unit area, but the species could be expected to contribute significant volumes to the mixed hardwood stands only on the best sites in the mountains. Estimated total cubic volumes in 1980 in the mountains of three States are as follows *(19)*:

	m^3	ft^3
	thousands	
Georgia	81	2,861
North Carolina	1171	41,353
South Carolina	42	1,492

Rooting Habit—The rooting habit of Carolina silverbell has not been studied, but the root systems are known to be very persistent, because stumps sprout repeatedly when trees are cut from pastures *(8)*.

Reaction to Competition—Carolina silverbell grows as an understory tree over most of its range and as a codominant in the mountains. It is classed as a shade-tolerant tree. A moist, loamy, partially shaded soil makes the best seedbed for either natural or artificial regeneration, although the species has been found with mixed hardwoods which regenerated a large, burned area in eastern Tennessee *(7,23,24,26)*. In hemlock stands in western North Carolina, the species occurred with greater frequency on areas without a rhododendron cover than with *(25)*. It competes well with other species regenerating in gaps left by treefalls in Southern Appalachian forests *(29,36)*.

Damaging Agents—Carolina silverbell appears to be free of serious insect pests or diseases *(17,23)*.

Special Uses

The wood of Carolina silverbell has many fine properties which make it very desirable for veneer, cabinet work, carving, and turning. It is a favorite wood of craftsmen who make woodenware for the tourist trade. The wood is soft with white or creamy sapwood and light cherry-colored heartwood streaked with white. Wood from larger trees has been sold as cherry or birch and the wood is acceptable for pulping along with other hardwood species. In the tourist trade it is sold under such names as bellwood, tisswood, and boxelder *(14,17,18,26)*.

Squirrels use Carolina silverbell seeds for food and the trees for dens. The heavy flower crops in spring are very attractive to bees, and eastern Tennessee beekeepers speak highly of the species as a honey plant *(12,22,33)*.

Carolina silverbell is best known for its ornamental qualities. Its heavy crop of white, bell-shaped flowers in the spring and its small to medium growth habit make it a favorite for small gardens, lawns, patios, and tubs. It was first cultivated in 1756 and since has been successfully cultivated in the Eastern United States, California, and western and central Europe *(23,30)*. It transplants well as balled and burlapped or container-grown stock *(11)*. Its best ornamental uses include border plantings in combination with low-growing plants such as azaleas, at corners of buildings and against a background of large evergreens. Its blooms can best be seen from below, so the tree needs to be conveniently accessible. Sprays of the flowers go well with cut-flower arrangements *(2,16,19,34)*. The large form from the mountains should not be used in small gardens but can be used with delightful results for street plantings, although it is not quite as hardy as the smaller form. Some trees have predominantly pink flowers, but a shady site may be required to produce this trait *(11,20,34)*.

Genetics

The first published description of Carolina silverbell appeared in 1731 in Mark Catesby's *Natural History of Carolina (17)*. Linnaeus made a taxonomic description of it in 1759 and named it *Halesia carolina* L. There is evidence that the specimen used by Linnaeus may have been a different species; nevertheless, *Halesia carolina* is the name currently accepted. The genus has two other species with limited distribution in the southeastern and southern Piedmont and Coastal Plain. They are *H. parviflora* Michx. and *H. diptera* Ellis. All have n=12 chromosomes *(7,9,27,31)*.

No studies on population differences in this species have been reported. However, its wide and discontinuous distribution likely has produced significant variation among and within populations over its range.

The large form of Carolina silverbell that grows in the southern Appalachian Mountains was at one time considered to be a separate species from the smaller form that occupies the rest of the range. It was given the name *H. monticola* (Rehd.) Sarg. but it differs from the smaller form only in size, and recent authors consider it synonymous with *H. carolina* (*7,11,20,34*).

Intergradation between *H. carolina* L. and *H. parviflora* Michx. (little silverbell) is suspected in the northern Coastal Plain where their distributions overlap (*7*).

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Ilex opaca Ait. American Holly

Aquifoliaceae Holly family

H. E. Grelen

When the Pilgrims landed the week before Christmas in 1620 on the coast of what is now Massachusetts, the evergreen, prickly leaves and red berries of American holly *(Ilex opaca)* reminded them of the English holly *(Ilex aquifolium)*, a symbol of Christmas for centuries in England and Europe *(13,26)*. Since then American holly, also called white holly or Christmas holly, has been one of the most valuable and popular trees in the Eastern United States for its foliage and berries, used for Christmas decorations, and for ornamental plantings.

Habitat

Native Range

From the maritime forests of Massachusetts, holly (fig. 1) is scattered along the coast to Delaware. It

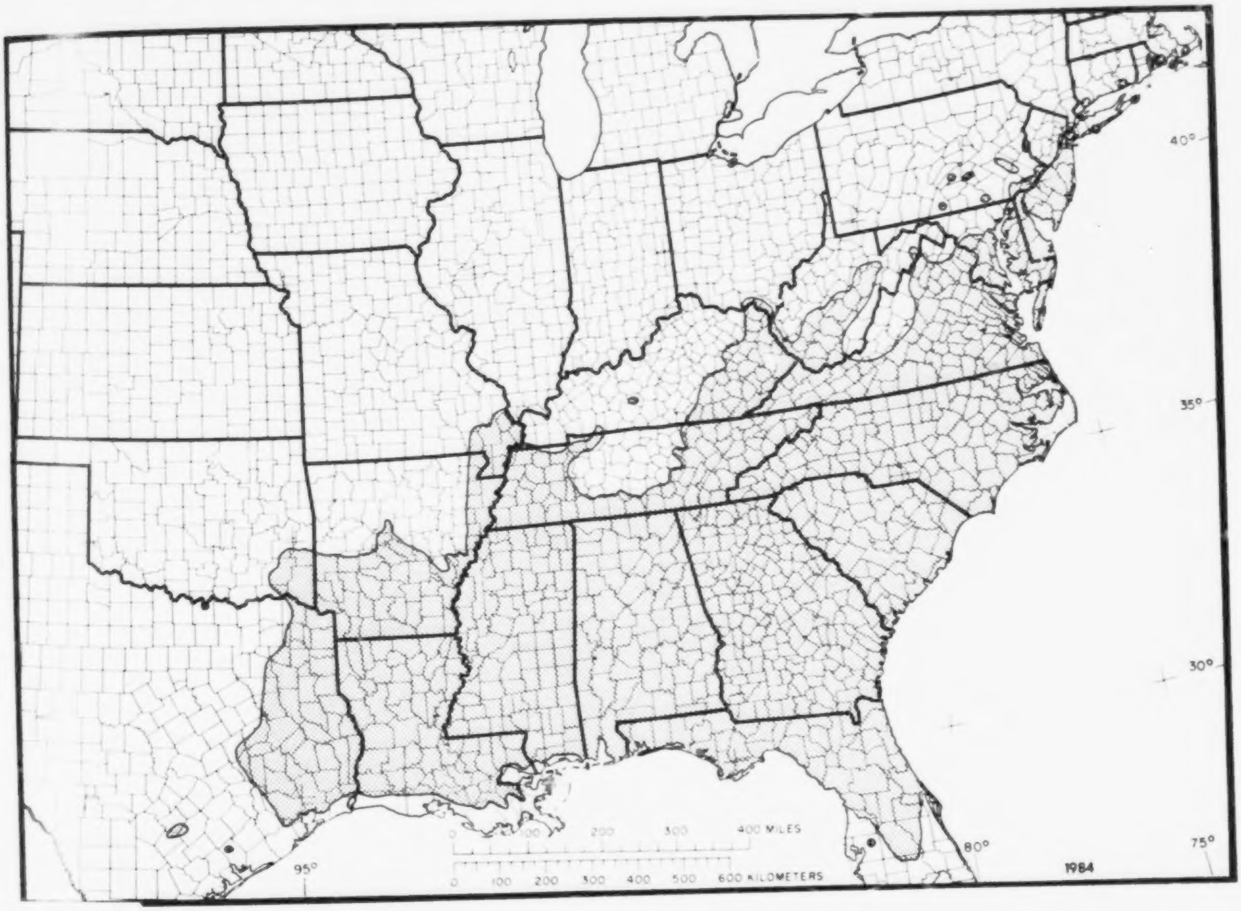

Figure 1—*The native range of American holly.*

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grows inland into several Pennsylvania counties and abundantly southward throughout the coastal plain, Piedmont, and Appalachian system. The range extends south to mid-peninsular Florida, west to eastern Texas and southeastern Missouri *(20)*. It corresponds roughly to the combined ranges for loblolly and shortleaf pines.

Climate

Like the southern pines, American holly is primarily a plant of the humid Southeast. Annual precipitation throughout its range is 1020 to 1650 mm (40 to 65 in) with over 2030 mm (80 in) in the southern Appalachians. Growing season varies from about 150 days in the Appalachian Mountains, the northeastern limit of the range, to almost yearlong in the central Florida peninsula. Average minimum temperature in the coastal plain portion of its range is above -18° C (0° F) but in the mountains of West Virginia, holly grows where the average low temperature is below -23° C (-10° F) *(20)*. Holly cultivars in a northern Ohio arboretum, north of its natural range, have survived -29° C (-20° F) *(12)*. American holly is the hardiest known broadleaf evergreen tree *(23)*.

Soils and Topography

Holly survives on a wide variety of soils from near sterile Inceptisols of Atlantic sandy beaches to fertile but thin mountain Ultisols to an elevation of approximately 915 m (3,000 ft) *(8)*. Largest trees are found in the rich bottom lands and swamps of the coastal plain (fig. 2). Growth is best on moist, slightly acid, well-drained sites such as upland pine sites and hammocks. Trees will not survive flooding or saturated soils for more than 17 percent of the growing season *(31)*. In the northeastern portion of its range, holly is found on sandy coastal soils or dry gravelly soils farther inland *(16)*.

Associated Forest Cover

In longleaf pine-slash pine *(Pinus palustris—P. elliottii)* forests of the coastal plain, frequent prescribed fires are more limiting to the presence of American holly than site. Within that timber type, therefore, association is mainly with trees of bottom lands, swamps, or other sites not subject to burning. In the loblolly pine-shortleaf pine and upland hardwood types where fire is not so common, holly, as well as numerous other hardwoods, is found beneath the pines on a wide range of sites. Because of its slow growth and relatively short stature, holly is seldom dominant. It is an understory component of a number of forest cover types *(10)*. Common associates of holly in various parts of its geographic range are shown in table 1.

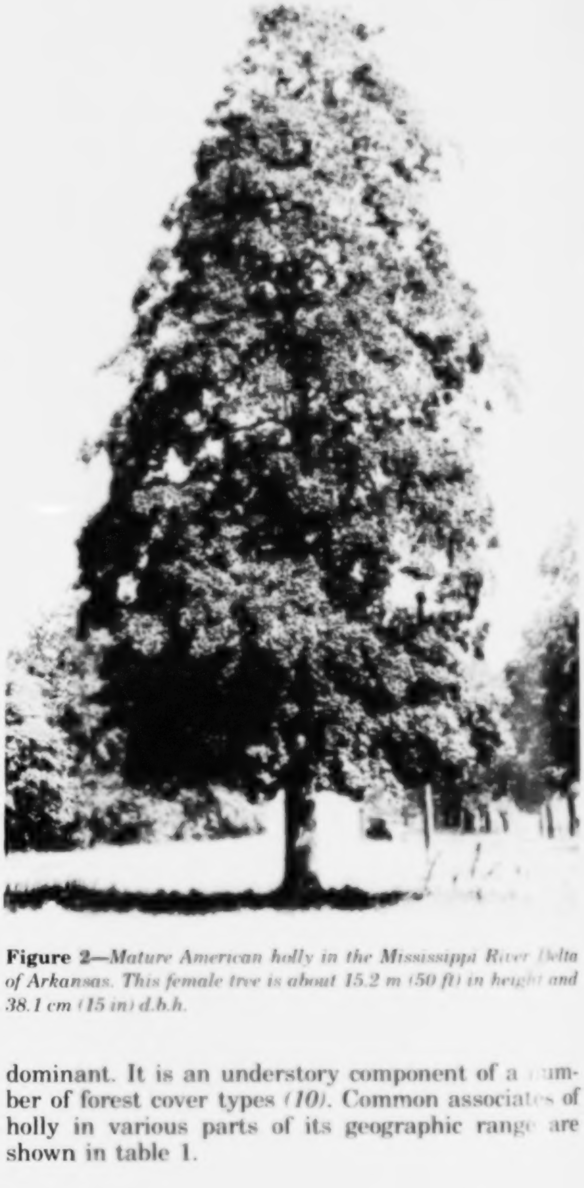

Figure 2—*Mature American holly in the Mississippi River Delta of Arkansas. This female tree is about 15.2 m (50 ft) in height and 38.1 cm (15 in) d.b.h.*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Hollies are dioecious; male (staminate) and female (pistillate) flowers, similar in appearance, with four to six small white petals, are produced on separate plants on the current season's growth. The male-to-female ratio for

Table 1—Trees commonly associated with American holly on various sites throughout its range

Tree species	Range[1]
Sweetgum *(Liquidambar styraciflua)*	A, C, D, F, G, I
Flowering dogwood *(Cornus florida)*	A, B, D, G, I
American beech *(Fagus grandifolia)*	A, B, E, G, I
Red maple *(Acer rubrum)*	A, F, G, H
White oak *(Quercus alba)*	B, C, F, G
Water oak *(Quercus nigra)*	A, C, G, I
Hickory *(Carya spp.)*	C, D, G
White ash *(Fraxinus americana)*	C, D, F
Yellow-poplar *(Liriodendron tulipifera)*	D, F, G
Black tupelo *(Nyssa sylvatica)*	A, D, G
Southern red oak *(Quercus falcata)*	A, F, G
Post oak *(Quercus stellata)*	A, C, H

[1] Key to range symbols:
A East Texas *(15,25)*
B Southeast Louisiana *(7)*
C Mississippi River Delta *(24)*
D Georgia Piedmont *(24)*
E Kentucky, western hills *(24)*
F Southeast Pennsylvania *(24)*
G Virginia Coastal Plain *(35)*
H New Jersey and New York, maritime forests *(28)*
I North-central Florida *(29)*

1,930 seedlings from 10 randomly chosen, open-pollinated pistillate trees was 1.03 to 1.00 after 9 years had elapsed and all seedlings had produced flowers. Flowering began as early as age 3 and the latest bloomed at age 9, staminate plants flowering somewhat earlier on the average than pistillate. For this reason, the male-to-female ratio at age 5 was about 5 to 1 *(5)*.

Flowering begins in April in the southern part of the range of American holly, and in June at the northern limits. Pollination is accomplished by insects, including bees, wasps, ants, yellowjackets, and night-flying moths *(3)*. Staminate trees should be planted close to fruit-producing trees *(34)*. Although some female hollies are apparently isolated by distance from pollen-bearing trees, good fruit crops are produced regularly. The fruit, commonly called "berries," are technically four-seeded drupes or pyrenes. They ripen from September through December and remain on the tree through most of the winter unless consumed by birds or other wildlife. The fruit is round to ellipsoid, about 6 to 12 mm (0.25 to 0.50 in) in diameter, and bright—but not shiny—red, orange, or occasionally yellow in color.

The four seeds in each fruit are bony with a coarsely reticulated, ridged surface *(34)*. Seed germination is very slow, requiring from 16 months to 3 years in nature. Germination tests over a 2.5-year period indicated only 33 to 56 percent germination capacity. Over winter storage or cold, moist stratification improves germination. Sowing immediately after collection has been recommended although complete germination does not occur until the second or third spring *(4)*.

Seed Production and Dissemination—Seed production may be low in years of heavy spring rain, as rain can diminsh the wide dissemination of pollen. A late frost can kill the spring flowers, eliminating a fruit crop. Frequent prescribed burning also drastically reduces fruit production. Such crop failures are rare and localized, however, and an abundance of seed can be found each year *(19,24)*. Clean seeds average approximately 61,730/kg (28,000/lb) and about four units (by weight) of fruit yield one unit of clean seeds *(4)*. Seeds are dispersed mainly by birds and small mammals.

Seedling Development—Germination is epigeal. Following germination, holly seedlings rapidly develop a taproot and numerous lateral roots. American holly is very shade tolerant and may become established from bird droppings in the understory of upland pine plantations or bottom land hardwoods. It is very susceptible to fire and may be completely lacking in regularly or even occasionally burned forests *(35)*. Initial growth is slow, averaging about 1.8 m (6 ft) in 16 years under medium shade *(32)*. The bark is easily injured by fire and even large trees may be killed by light fires in the understory. Fastest growth of American holly was probably achieved in a North Carolina holly plantation; after 9 years of cultural practices such as mowing, mulching, and fertilizing, 10-year-old hollies averaged about 6.7 m (22 ft) in height and 3.7 m (12 ft) in crown spread and produced abundant fruit *(24)*.

Vegetative Reproduction—Young holly trees usually sprout if the tops are removed by cutting or burning. Because of a taproot and a profilic lateral root system, young hollies can be transplanted without much difficulty *(6)*. Transplanting should be done during the dormant season, usually November through March. Small plants may be dug bare-rooted if roots are kept moist, but larger plants should be balled and burlapped *(34)*. When wild hollies are transplanted from the woods, tops should be severely pruned and most of the remaining leaves removed *(16)*. Small trees should be allowed to flower before transplanting to ensure the selection of fruit-bearing individuals. Root pruning to a depth of 0.6 to 0.9 m (2 to 3 ft), a year before lifting, improves transplanting success *(27)*. In Ohio, outside the natural range of American holly, better outplanting success has been obtained with plants 60 to 120 cm (24 to 48 in) tall than those 30 cm (12 in) or less, because of winterkill of the younger plants *(11)*. Holly can be produced from cuttings taken in August or September and December. Cuttings should be taken from the current season's ripened wood, with a small section of 2-year-old wood including several leaves. Cuttings should be set slanting in about 15 cm (6 in) of peatmoss and soil moisture, with the leaves lying flat on the surface. Treating with indolebutyric acid (IBA) and growing under high humidity with bottom heat is also recommended *(6,24)*. "Quick dips" in IBA at high concentrations (up to 20,000 p/m) are recommended for cultivars that are normally hard to propagate *(27)*. Root cuttings are unsatisfactory.

Sapling and Pole Stages to Maturity

Growth and Yield—Because of its intolerance of fire, holly is found as scattered trees, even on good holly sites. Its slow growth and limby habit detract from its timber value. American holly under intensive culture is capable of 0.9 to 1.2 m (3 to 4 ft) of height growth per year *(3)*.

Holly dominates some of the maritime forests of the Atlantic coast near the northern limit of its range, associated with salt-intolerant species such as black cherry *(Prunus serotina)*, eastern redcedar *(Juniperus virginiana)*, and hackberry *(Celtis occidentalis)*. One of the best developed coastal stands reported was at Sandy Hook in New Jersey, where 97 percent of the tree basal area of a 30-ha (74-acre) forest was American holly. The oldest holly was 144 years old and 62 cm (24 in) in d.b.h. Height of holly trees in these sandy coastal forests ranges from 4.6 to 9.1 m (15 to 30 ft). Older trees or those on better sites may reach 15.2 m (50 ft) *(28)*.

The "national champion" American holly, in the Congaree Swamp of South Carolina, is 30.2 m (99 ft) tall, with a circumference of 248 cm (98 in), a trunk diameter of 79 cm (31 in), and a crown diameter of 12.2 m (40 ft) *(2)*. Hollies 30 to 90 cm (24 to 36 in) in diameter measured near the ground are common in the Mississippi River Delta *(24)*. Trees 30.5 m (100 ft) tall and 122.0 cm (48 in) in d.b.h. have been recorded *(18)*, but such trees were over 100 years old.

Rooting Habit—No information available.

Reaction to Competition—Holly is classed as very shade tolerant and can survive in the understory of most forest canopies, but growth may be slowed and flowering and fruit set reduced under shade *(22)*. Leaf area increased and leaves were greener under shade *(30)*. In a mesic pine-hardwood forest of east Texas, dominated by loblolly pine *(Pinus taeda)*, southern magnolia *(Magnolia grandiflora)*, American beech *(Fagus grandifolia)*, white oak *(Quercus alba)*, and water oak *(Q. nigra)*, holly was the principal understory species *(15)*. Its slow growth allows faster growing species of the same age to overtop it. Shade and root competition in natural stands reduced average height of hollies at age 16 by about 0.3 m (1 ft) in medium shade and 0.61 m (2 ft) in heavy shade, compared with those growing in full sunlight. Crown area was reduced by one-third under medium shade and by more than one-half under heavy shade *(32)*.

Damaging Agents—The greatest damage to holly trees is indiscriminate harvesting of foliage with berries for Christmas decorating. Before laws were passed in Maryland and Delaware to protect the holly, there was a "roadside" market for holly vandalized from trees that did not belong to harvesters. Trees were left mutilated and many died *(17)*.

Fire is another deadly enemy of American holly. Most commercial pine timberland is burned often enough to eliminate holly seedlings or sprouts, especially where livestock graze. Burning where hollies are in the midstory can seriously damage the bark and kill trees. Three annual fires in a southern pine forest reduced the number of fruit-producing holly trees by 95 percent *(19)*.

The thick evergreen leaves, which remain on the trees until the spring of their third year *(18)*, are year-long hosts to many foliage diseases and insects. Few threaten the health of the trees, but many may reduce the esthetic and commercial value of the foliage. Diseases include 14 species of leaf spot fungi, six species of black mildews, two powdery mildews, and one rust. The most common and widespread of the leafspots are caused by the fungi *Cercospora pulvinula, Phacidium curtissii, Phyllosticta opaca*, and *Physalospora ilicis*. The rust *Chrysomyxa ilicina* is known only from the southern Appalachian area. Hollies of the northeast are subject to a serious leaf and twig blight caused by *Corynebacterium ilicis* *(16)*.

Although nearly 30 species of insects are known to attack holly, only a few are serious pests. The southern red mite *(Oligonychus ilicis)* causes a reduction in leaf and twig growth and undesirable foliage color. The native holly leafminer *(Phytomyza ilicicola)* can damage foliage severely, causing leaves to drop prematurely. The holly midge *(Asphondylia ilicicola)* feeds on the berries causing them to remain green in color. Several species of scale insects feed on holly, including the holly scale *(Asterolecanium puteanum)* *(1,24)*.

Strong winds cause spines of mature leaves to puncture other leaves, rendering the foliage less valuable for decoration *(24)*. In northern portions of its range, twigs and branches can be killed during extreme cold periods *(12)*, although holly is quite hardy *(23)*.

Holly is more resistant to damage from salt spray than associated woody species in the maritime forests of New England, enabling it to dominate coastal stands *(29)*. Hollies are intolerant of flooding and may die if their roots are inundated for a period of several weeks *(31)*.

Special Uses

The attractiveness of its foliage is American holly's principal value, whether as a forest tree, planted ornamental, or Christmas decoration. The development of commercial holly orchards and the education of landowners in the value and harvesting of holly foliage have lessened the exploitation of wild hollies *(13)*.

The wood of American holly is tough and hard but not strong. It is close-grained and moderately heavy, weighing about 640.7 kg/m^3 (40 lb/ft^3). Specific gravity is 0.61 (oven-dry) and about 0.50 green. It is one of the whitest woods known, with white sapwood and ivory-white heartwood. Growth rings are almost indistinct. The wood is used for veneer and to a limited extent as pulpwood and lumber. Greatest use of the wood is for specialty items such as fancy cabinet inlays, small pieces of furniture, brush backs, handles, novelties, wood engravings, scroll work, woodcuts and carvings, and measuring scales and rules for scientific instruments; when dyed black to resemble ebony, it is used for piano keys, violin pegs, and fingerboards *(6,18,33)*.

Birds are the principal consumers of the fruit, although deer, squirrels, and other small mammals also eat them. Cattle sometimes browse the foliage. At least 18 species of birds including songbirds, mourning doves, wild turkeys, and the bobwhite are known to eat the fruit *(14,34)*. Perhaps the most important in seed dispersal, however, are the large winter-migrating flocks of small birds such as the cedar waxwing and American goldfinch. The complete stripping of all berries from a 10.7 m (35 ft) tall holly in a few seconds by a flock of cedar waxwings has been observed.

Despite the presence of saponins in the leaves and berries, American holly is not considered poisonous to man or animals *(36)*. Although not as well known as gallberry *(Ilex glabra)* as a honey plant, its nectar makes excellent honey *(24)*.

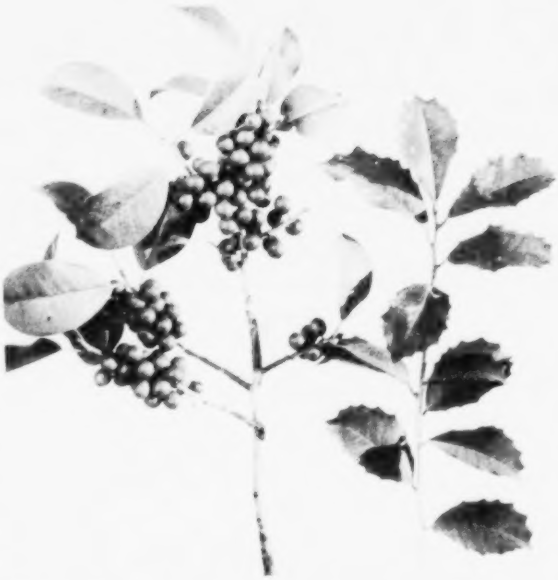

Figure 3—*Two branches from the same American holly tree, showing variation in leaf spininess. Branch with spineless leaves and fruit is from upper canopy; branch with toothed leaves is from basal sprout. (Courtesy Dr. Clair A. Brown)*

Genetics

Population Differences

American holly has 36 chromosomes, differing from the basic number for the genus *Ilex* of 9 or 10 *(24)*. Although leaf spininess and fruit colors vary, the coastal-dune hollies are usually smaller than those on the rich bottom lands of the Mississippi River Delta. Only one botanical variety other than the typical variety is recognized *(21)*. Dune holly *(Ilex opaca* var. *arenicola)* grows on deep sandy soils in north and central Florida. It has lanceolate or oblanceolate leaves with forward-pointing teeth and oval, shallowly grooved nutlets. Yellow-fruited holly, once named a variety, is now considered only the expression of the recessive yellow color gene present in nearly all red-fruited hollies. Spineless leaves were once the basis for segregating another variety but the trait is highly variable; spiny and spineless leaves often grow on the same plant *(34)* (fig. 3).

More than 1,000 cultivars of American holly have been named, although not all have been registered with the International Registration Authority. These do not necessarily represent different forms of *Ilex opaca*; many were selected because of unusual growth habit, fruit color, size or shape, or degree of leaf spininess *(9)*.

Hybrids

Topel holly (*I.* × *attenuata* Ashe) is a hybrid of *I. opaca* and dahoon holly (*I. cassine*), with long spiny-pointed leaves, that grows in South Carolina and northwestern Florida *(21,34)*. Several cultivars registered under *Ilex opaca*, such as Foster, Hume, Savannah, and East Palatka, are actually *I.* × *attenuata (9)*. Crosses have occurred between American holly and myrtle dahoon (*I. myrtifolia*), which, like dahoon holly, is an evergreen, red-fruited shrub or small tree found on wet sites of the coastal plain *(24)*.

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Juglans cinerea L. Butternut

Juglandaceae Walnut family

George Rink

Butternut (*Juglans cinerea*), also called white walnut or oilnut, grows rapidly on well-drained soils of hillsides and streambanks in mixed hardwood forests. This small to medium-sized tree is short lived, seldom reaching the age of 75. Butternut is more valued for its nuts than for lumber. The soft coarse-grained wood works, stains, and finishes well. Small amounts are used for cabinetwork, furniture, and novelties. The sweet nuts are prized as a food by man and animals. Butternut is easily grown but must be transplanted early because of the quickly developing root system.

Habitat

Native Range

Butternut (figs. 1, 2) is found from southeastern New Brunswick throughout the New England States except for northwest Maine and Cape Cod. The range extends south to include northern New Jersey, western Maryland, Virginia, North Carolina, northwestern South Carolina, northern Georgia, northern Alabama, northern Mississippi, and Arkansas. Westward it is found to central Iowa and central Minnesota. It grows in Wisconsin, Michigan, and northeast into Ontario and Quebec. Through most of its range butternut is not a common tree, and its frequency is declining *(4)*. The ranges of butternut and black walnut (*Juglans nigra*) overlap, but butternut occurs farther north and not as far south as black walnut.

Climate

Climatic conditions within the botanical range of butternut vary widely. Mean annual temperature ranges from 16° C (60° F) in Alabama to 4° C (40° F) in New Brunswick, with an average maximum of 41° C (105° F) and minimum of -34° C (-30° F). Annual precipitation ranges from 630 mm (25 in) in southeastern Minnesota to 2030 mm (80 in) in the southern Appalachians. The frost-free period is 210 days in the southern part of the range and 105 days in the northern part *(6)*.

Butternut is generally considered to be more winter-hardy than black walnut.

Soils and Topography

Butternut grows best on streambank sites and on well-drained soils; it is seldom found on dry, compact, or infertile soils. It grows better than black walnut, however, on dry, rocky soils, especially those of limestone origin.

Butternut is found most frequently in coves, on stream benches and terraces, on slopes, in the talus of rock ledges, and on other sites with good drainage, primarily on soils of the orders Alfisols and Entisols. It is found up to an elevation of 1500 m (4,900 ft) in the Virginias, at much higher altitudes than black walnut *(4,18)*.

Associated Forest Cover

Butternut is found with many other tree species in several hardwood types in the mixed mesophytic forest. It is an associated species in the following four northern and central forest cover types *(5)*: Sugar Maple–Basswood (Society of American Foresters Type 26); Yellow-Poplar–White Oak–Northern Red Oak (Type 59); Beech–Sugar Maple (Type 60); and River Birch–Sycamore (Type 56). Commonly associated trees include basswood (*Tilia* spp.), black cherry (*Prunus serotina*), beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), elm (*Ulmus* spp.), hemlock (*Tsuga canadensis*), hickory (*Carya* spp.), oak (*Quercus* spp.), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), yellow-poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), and yellow birch (*Betula alleghaniensis*). In the northeast part of its range, it is often found with sweet birch (*Betula lenta*) and in the northern part of its range it is occasionally found with white pine (*Pinus strobus*) *(4,15)*. Forest stands seldom contain more than an occasional butternut tree, although in local areas it may be abundant. In the past, West Virginia, Wisconsin, Indiana, and Tennessee have been the leading producers of butternut timber.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Butternut flowers from April to June, depending upon location. The species is monoecious; male flowers are slender catkins that develop from axillary buds and female flowers are short terminal spikes borne on current

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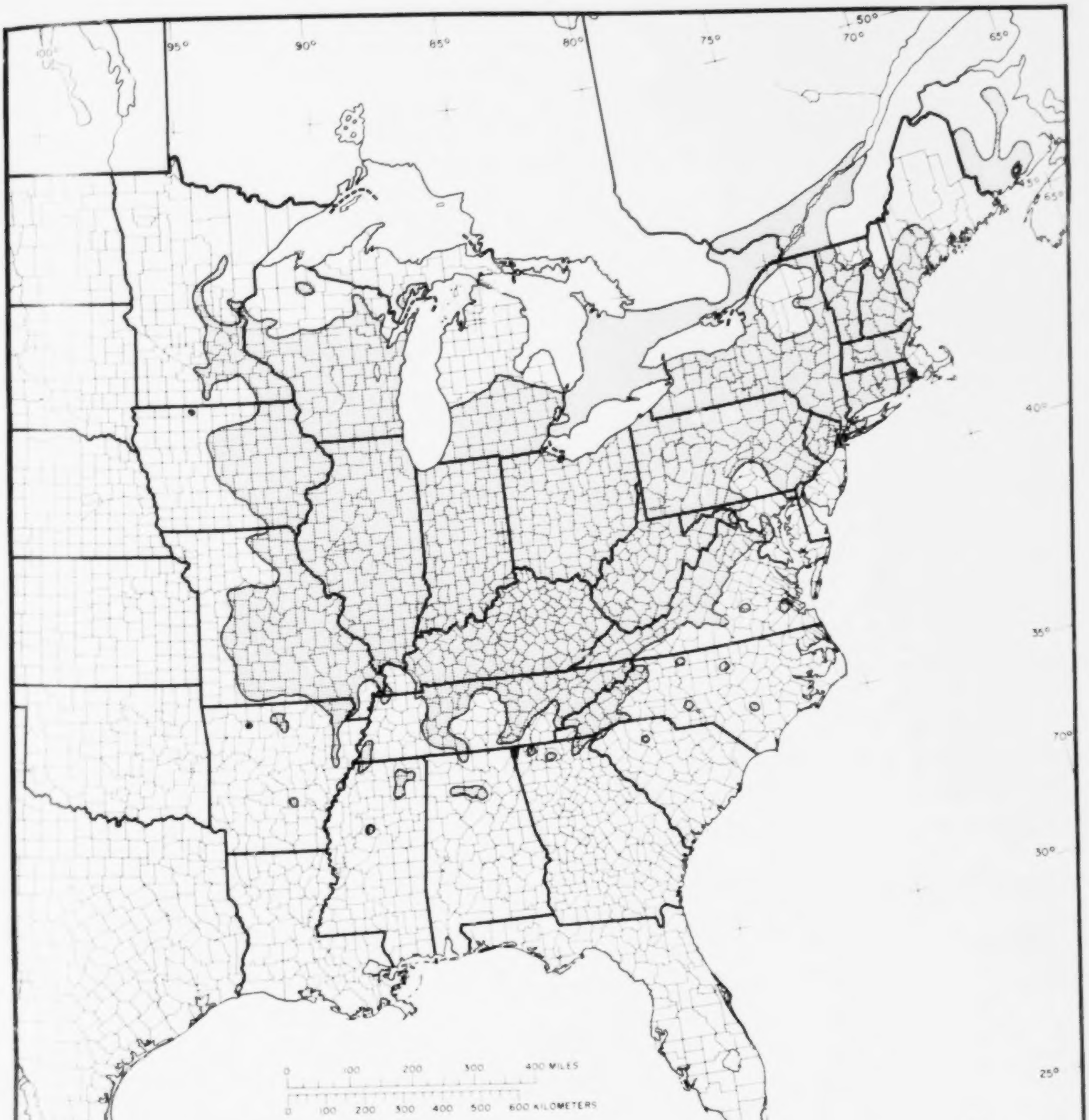
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Figure 1—*The native range of butternut.*

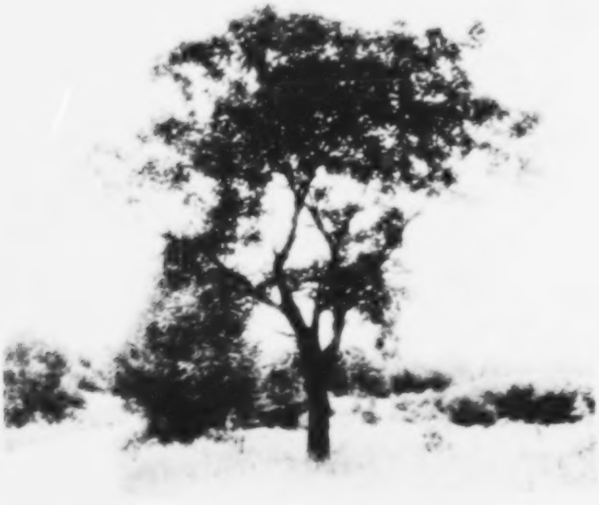

Figure 2—*Young butternut in the White Mountain National Forest, NH.*

year's shoots. Flowers of both sexes do not usually mature simultaneously on any individual tree *(3)*.

The fruit is an oblong-ovoid pointed nut, 3.8 to 5.5 cm (1.5 to 2.2 in) long, that matures in September and October of the year of pollination. Nuts occur singly or in clusters of from 2 to 5. The kernel or seed of the nut is sweet, oily, and edible. The nut is enclosed by an indehiscent husk that contains a glandular pubescence on the surface. The fruit usually remains on the tree until after leaf fall *(3)*.

Seed Production and Dissemination—Commercial seed-bearing age begins at about 20 years and is optimum from age 30 to 60 years. Good crops can be expected every 2 to 3 years, with light crops during intervening years. Thrifty trees may yield 9 to 35 liters (0.25 to 1 bushel) of cleaned seeds. A high percentage of mature seeds are sound, but high premature seed losses in butternut have been reported. Possible causes include consumption by insects, birds, and rodents as well as natural pollination failures due to a lack of pollinating trees in the immediate vicinity *(4,10,14,21)*.

Upon ripening, seeds are dispersed by gravity and by squirrels and other rodents. At this time, the seeds are dormant. Cold stratification for 90 to 120 days at temperatures of 20° to 30° C (68° to 86° F) overcomes dormancy *(3)*.

Seedling Development—Seeds of butternut usually germinate in the spring following seedfall. Germination is hypogeal. Seedlings develop a taproot on all sites except the most shallow soils, but the taproot is much less pronounced than on black walnut. In general, butternut seedlings have more fibrous root systems than black walnut.

Vegetative Propagation—Stumps of young butternut trees and saplings are capable of sprouting. Also, butternut can be propagated by grafting, although the techniques have not yet been perfected. Various degrees of success have been demonstrated with intra-specific as well as inter-specific grafting in the genus *(9)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Butternut grows fast, especially as a seedling, although it usually does not live longer than 75 years and is short lived in relation to its common tree associates.

Mature trees rarely reach a height of more than 30 m (100 ft) and a d.b.h. of 91 cm (36 in). Average-sized trees are from 12 to 18 m (40 to 60 ft) in height and 30 to 61 cm (12 to 24 in) in d.b.h. *(4)*.

Rooting Habit—On favorable sites the root system is deep, but it also may be widespreading.

Reaction to Competition—Although young trees may withstand competition from the side, butternut does not survive under shade from above. It must be in the overstory to thrive and, therefore, is classed as intolerant of shade and competition.

Like other members of the Juglandaceae family, butternut produces a substance called juglone, a naphthoquinone that is selectively toxic to associated vegetation. Greatest concentrations of juglone are in root tissue and fruit husks with lesser amounts in leaves, catkins, buds, and inner bark *(12,13)*.

Within its optimum range and on good sites, butternut is usually considered a desirable component of forest stands; it has been classed as a "less desirable" tree in southern Appalachian coves *(4)*.

Damaging Agents—Insect enemies of butternut are often pests of associated trees as well. Some insects commonly found on butternut include wood borers, defoliators, nut weevils, lacebugs, husk flies, and bark beetles. The most serious insect pest at this time is the butternut curculio *(Conotrachelus juglandis)*, which injures young stems and fruit *(8,21)*.

The most serious disease of *Juglans cinerea* is butternut decline or butternut canker. In the past the causal organism of this disease was thought to be a fungus, *Melanconis juglandis*; but now this fungus is has been associated with secondary infections and the primary causal organism of the disease has been identified as another species of fungus, *Sirococcus clavigignenti-juglandacearum*. Symptoms of the disease include dying branches and stems. Initially, cankers develop on branches in the lower crown. Spores developing on these dying branches are spread by rainwater to tree stems. Stem cankers develop 1-3 years after branches die. Tree tops killed by stem-girdling cankers do not resprout (*19,20*). Diseased trees usually die within several years (*11,16*). The disease is reported to have eliminated butternut from North and South Carolina (*1*). The disease is also reported to be spreading rapidly in Wisconsin; between 1978 and 1983 the incidence of butternut canker in a young, isolated plantation increased exponentially from 5 percent in 1976 to 76 percent in 1983 (*20*). By contrast, black walnut seems to be resistant to the disease.

Bunch disease also attacks butternut. Currently, the causal agent is thought to be a mycoplasmalike organism. Symptoms include a yellow witches' broom resulting from sprouting and growth of axillary buds that would normally remain dormant. Infected branches fail to become dormant in the fall and are killed by frost; highly susceptible trees may eventually be killed. Butternut seems to be more susceptible to this disease than black walnut (*2,17*).

The common grackle has been reported to destroy immature fruit and may be considered a butternut pest when populations are high (*14*).

Butternut is very susceptible to fire damage, and although the species is generally windfirm, it is subject to frequent storm damage (*4*).

Special Uses

Cultivars of this species have been selected for nut size and for ease of cracking and extracting kernels. Several cultivars have been named (*14*). Nuts are especially popular in New England for making maple-butternut candy. Small amounts of wood are used for cabinets, toys, and novelties.

Genetics

Butternut hybridizes with English walnut (*Juglans regia* L.) to produce *J.* × *quadrangulata* (Carr.) Rehd. It also crosses with Japanese walnut *J. ailantifolia* Carr. to produce *J.* × *bixbyi* Rehd. Butternut is also reported to successfully hybridize with little walnut (*J. microcarpa* Berland.) and Manchurian walnut (*J. mandshurica* Maxim.) (*6,14*). Reports of crosses between butternut and black walnut have not been substantiated. Butternut is thought to have a haploid chromosome number of 16.

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Juglans nigra L. Black Walnut

Juglandaceae Walnut family

Robert D. Williams

Black walnut (*Juglans nigra*), also called eastern black walnut and American walnut, is one of the scarcest and most coveted native hardwoods. Small natural groves frequently found in mixed forests on moist alluvial soils have been heavily logged. The fine straight-grained wood made prize pieces of solid furniture and gunstocks. As the supply diminishes, the remaining quality black walnut is used primarily for veneer. The distinctive tasting nuts are in demand for baked goods and ice cream, but people must be quick to harvest them before the squirrels. The shells are ground for use in many products.

Habitat

Native Range

Black walnut (figs. 1, 2) typically grows as scattered individual trees or in small groups throughout the central and eastern parts of the United States. Although it is found on a variety of sites, black walnut grows best on good sites in coves and well-drained bottoms in the Appalachians and the Midwest. Its natural range extends from western Vermont and Massachusetts west through New York to southern Ontario, central Michigan, southern Minnesota, eastern South Dakota and northeastern Nebraska; south to western Oklahoma and central Texas; excluding the Mississippi River Valley and Delta, it ranges east to northwestern Florida and Georgia *(28,29)*. On the western fringe of its range in Kansas, walnut is fairly abundant and frequently makes up 50 percent or more of the basal area in stands of several hectares *(21)*.

Climate

The growing season within the range of black walnut ranges from 140 days in the north to 280 days in western Florida *(10,43)*. Annual precipitation is less than 640 mm (25 in) in northern Nebraska and 1780 mm (70 in) or more in the Appalachians of Tennessee and North Carolina. Mean annual temperatures range from about 7° C (45° F) in the north to 19° C (67° F) in the south. Temperatures as low as -43° C (-45° F) have occurred where walnut grows, but few races of black walnut can tolerate such low temperature. Within black walnut's optimum range, the average annual temperature is about 13° C (55° F), the frost-free season is at least 170 days, and the average annual precipitation is at least 890 mm (35 in).

Soils and Topography

Black walnut is sensitive to soil conditions and develops best on deep, well-drained, nearly neutral soils that are generally moist and fertile *(10)*. These soils are in the orders Alfisols and Entisols. Although an Ohio study indicated that site index for black walnut was not significantly related to pH values between 4.6 and 8.2, site index was highest on limestone derived soils even though some of the soils were acid. Walnut grows best on sandy loam, loam, or silt loam textured soils but also grows well on silty clay loam soils *(31)*. Soils with these textures hold a large amount of water that is available to the tree during dry periods of the growing season. Internal drainage and depth to gravel are especially important site characteristics for black walnut. On well-drained soils, 76 cm (30 in) or more to mottling, 25-year-old trees were 6.6 cm (2.6 in) larger in d.b.h. than trees growing on imperfectly drained soils, 15 to 76 cm (6 to 30 in) to mottling. Twenty-five-year-old trees on deep soils, more than 102 cm (40 in) from surface to gravel, were 5.2 m (17 ft) taller and 6.4 cm (2.5 in) larger in d.b.h. than trees on shallow soils less than 102 cm (40 in) from surface to gravel *(30)*.

Walnut is common on limestone soils and grows especially well on deep loams, loess soils, and fertile alluvial deposits. It also grows well on good agricultural soils that do not have fragipans. Walnut grows slowly on wet bottom land and on sandy or dry ridges and slopes. Throughout its range, walnut generally reaches its greatest size and value along streams and on the lower portion of north- or east-facing slopes. This is particularly true near the limits of its natural range. In northeastern Kansas, site index on alluvial soils was 2.4 m (8 ft) greater than on residual soils and 2.7 m (9 ft) greater on northeast than on southwest aspects *(20)*.

Associated Forest Cover

Black walnut grows in many of the mixed mesophytic forests but is seldom abundant *(43)*. Usually it is found scattered among other trees; pure stands are rare, small, and usually located on the

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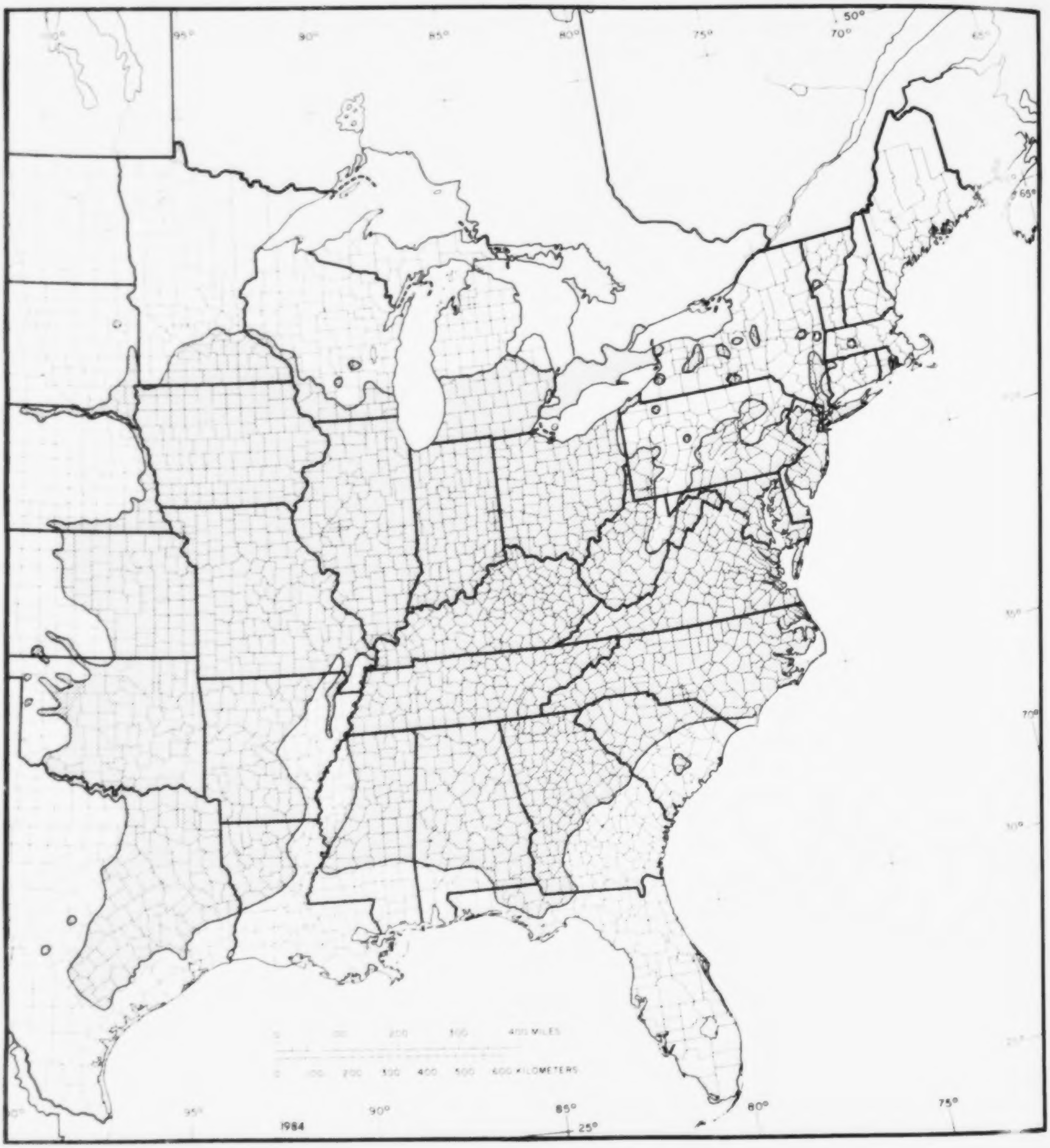
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Figure 1—*The native range of black walnut.*

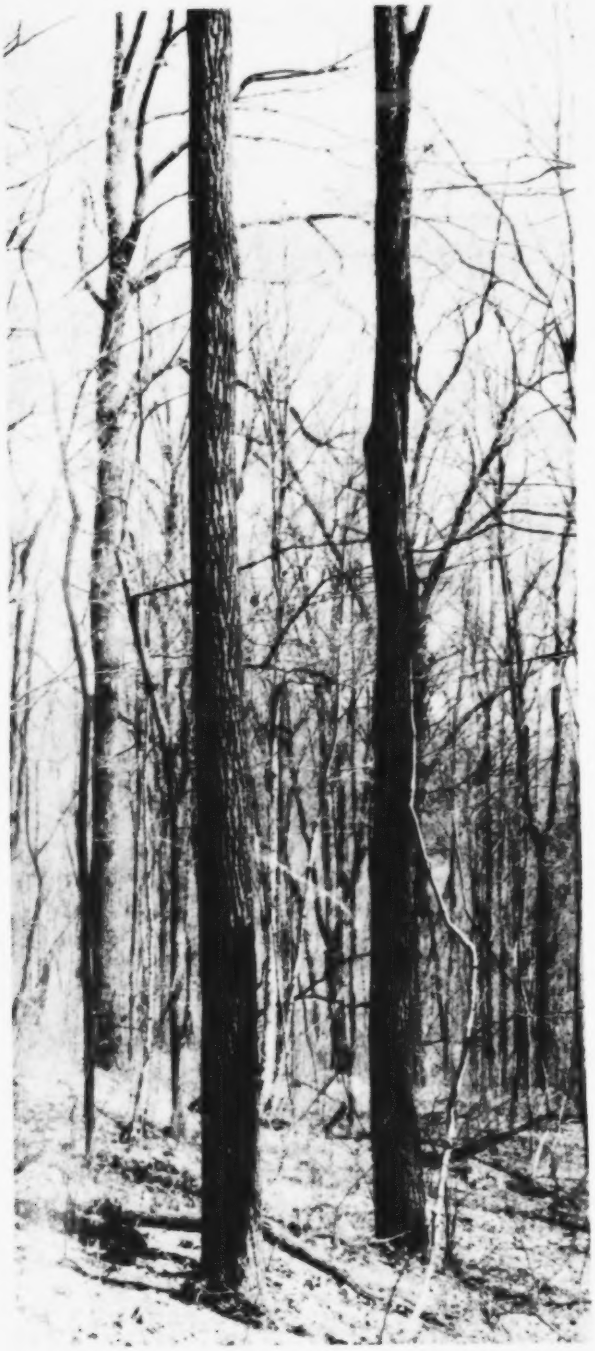

Figure 2—*Veneer quality trees on a good site.*

forest edge. Black walnut is a common associate in five forest cover types *(16)*: Sugar Maple (Society of American Foresters Type 27) in the central hardwood zone and the Appalachian highlands, Yellow-Poplar (Type 57) at lower elevations of the Appalachians, Yellow-Poplar–White Oak–Northern Red Oak (Type 59) at lower elevations, Beech–Sugar Maple (Type 60) in the Midwest, and Silver Maple–American Elm (Type 62) in southern Ontario washboard swamps where high and low ground intermingle.

It is also found as an occasional associated species in four cover types: Chestnut Oak (Type 44), White Oak–Black Oak–Northern Red Oak (Type 52), Northern Red Oak (Type 55) on moist sites, and Sassafras–Persimmon (Type 64) in older stands.

Chief associated species include yellow-poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), black cherry (*Prunus serotina*), basswood (*Tilia americana*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), oaks (*Quercus* spp.), and hickories (*Carya* spp.). Near the western edge of its range, black walnut may be confined to floodplains, where it grows either with American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), green ash (*Fraxinus pennsylvanica*), and boxelder (*Acer negundo*), or with basswood and red oak (*Quercus rubra*) on lower slopes and other favorable sites *(10)*.

No universal vegetative indicator of a good walnut site is known, but the presence of Kentucky coffeetree (*Gymnocladus dioicus*) seems to indicate such a site *(10,43)*. In general, where yellow-poplar, white ash, red oak, basswood, sugar maple, or slippery elm (*Ulmus rubra*) grow well, black walnut thrives also.

An antagonism between black walnut and many other plants growing within its root zone has been recognized and is attributed to juglone, a toxic substance found in the leaves, bark, nut husks, and roots of walnut trees *(32,42)*. Some tree species apparently are immune, but others, such as paper birch (*Betula papyrifera*), red pine (*Pinus resinosa*), white pine (*P. strobus*), Scotch pine (*P. sylvestris*), and apple (*Malus* spp.), reportedly are sensitive. Tomatoes are especially susceptible. In a laboratory study, juglone at high concentrations was lethal to four coniferous species, but seedling growth was actually promoted when exposed to minute concentrations *(19)*. Although tomatoes are especially susceptible to juglone, black walnut trees may be compatible with some agricultural crops and might even improve the growth of bluegrass (*Poa* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Depending on latitude, black walnut flowers generally begin to appear about mid-April in the South and progressively later until early June in the northern part of the natural range. Flowering and leafing out occur at approximately the same time and always early enough for possible damage by late spring frosts (*18,27*).

Walnut is monoecious; male flowers, which are slender catkins, develop from axillary buds on the previous year's outer nodes, while female flowers occur in short terminal spikes, ranging from a few to many, borne on the current year's shoots. Flowering is dichogamous, and protogyny (the female flowers appearing first) is more common than protandry (male flowers appearing first) (*33,34*). Because of its dichogamous flowering habit, self-pollination is unlikely. However, individual trees usually are not self-sterile; if they are not pollinated by neighboring trees, they may set self-fertilized seeds (*3*). Fertilization follows 2 to 5 days after pollination, succeeded by development of the husk, the shell, and finally by the seed itself (*18*).

Seed Production and Dissemination—The large edible nut ripens in September or October of the same year and drops shortly after the leaves fall. Good seed crops are produced irregularly, perhaps twice in 5 years. Open-grown trees may produce some seed when only 4 to 6 years old, but large seed crops do not occur until the trees are 20 to 30 years old (*28*). For example, at 10 years of age, a midwest plantation produced 28 kg of hulled nuts per hectare (25 lbs/acre), and by age 12 production had increased to 112 kg/ha (100 lb/acre). Best seed production begins when the trees are about 30 years old and continues for another 100 years. Seed is disseminated only short distances by gravity and animals.

In a Missouri study, seed production of trees about 28 years old and 19.3 cm (7.6 in) in d.b.h. was nearly doubled by release and fertilization (*40*). Trees released but not fertilized produced 13 percent more nuts than nonreleased trees.

Stratification for 90 to 120 days is required for optimum seed germination but the necessity and duration of stratification may vary by seed source (*46*). In Canada, 69 to 81 percent of nuts stratified 19 months germinated within 3 weeks of seeding, while 10 to 25 percent of nuts stratified 7 months germinated after 12 weeks (*48*). When nuts that had not germinated after 12 weeks in the seedbed following 7 months stratification were stratified for an additional 9 months, 81 percent germinated within 3 weeks. Many of the nuts stratified for 31 months germinated while in storage

Seedling Development—Germination is hypogeal (*46*). Young black walnut seedlings are intolerant of shade and are seldom found under dense tree canopies. Regeneration develops primarily from seed that squirrels bury and fail to recover. Normal winter temperatures usually cause the buried seeds to break dormancy the following spring, but germination is sometimes delayed until the second year.

Seedlings emerge in April or May the first or second spring after the seed is planted (*46*). On deep, rich, moist soils in coves or well-drained bottom land, seedlings may grow 91 cm (36 in) the first year and even more the second growing season. Although black walnut does not make as rapid height growth as yellow-poplar and white ash on good sites, it generally surpasses the oaks. In eastern Nebraska, near the western edge of its range, walnut made much better height growth than oaks or basswood on a prairie site (*10*). Walnut developed an excellent root system and was several times taller than the other tree species.

Height growth begins slowly in the spring, reaches a peak rate in late April and May, and is complete by the middle of July or the first of August. Black walnut loses its leaves somewhat earlier than other trees and has a growing period of from 115 to 135 days (*10*).

Because of its large taproot, planted walnut seedlings typically survive well. However, they require weed control during the first 2 or 3 years to grow well (*26*).

Vegetative Reproduction—If small black walnut trees are cut or killed back by fire, the stumps usually sprout. Sprouts originating near the root collar generally are free from defect but sprouts originating high on older stumps often develop heart rot or other decay from the parent stump.

Within the last few years the success of grafting and budding of walnut has increased substantially. From 80 to 100 percent success has been achieved by three grafting methods done in the greenhouse and growth chamber (*35*). In the field the success rate for inlay grafting, the best method tested, ranged from 33 to 83 percent. A consistent field survival of 70 to 90 percent for the outplantings of grafted stock is predicted if tested procedures are followed (*4*). Black walnut is compatible with several other *Juglans* species, either as a root stock or scion (*22*).

Sapling and Pole Stages to Maturity

Growth and Yield—On the best sites, young black walnut trees may grow 91 to 122 cm (36 to 48 in) in height per year (*28*). The best tree in a southern Indiana plantation at age 7 was 11.9 cm (4.7 in) d.b.h. and 7.6 m (25 ft) in height (*9*). In a southern Illinois plantation (site index 24.4 m or 80 ft at base age 50 years), the best tree was 21 cm (8.3 in) d.b.h. and 12 m (40 ft) tall at age 14 (*1*). However, the average size tree in the plantation was 12 cm (4.8

in) d.b.h. and 7 m (24 ft) tall. Even on less favorable sites (site index 21.3 m or 70 ft), trees reach heights of 12 to 15 m (40 to 50 ft) and diameters of 15 to 25 cm (6 to 10 in) in 20 years *(28)*. In contrast, diameter growth of black walnut planted on Kansas strip mine spoil banks averaged only 6 mm (0.25 in) per year and height growth averaged only 33.5 cm (13.2 in) per year during the first 10 to 12 years *(10)*. On Illinois spoil banks trees grew best on the lower slopes, on areas formed from limestone parent material and containing a high percentage of fine soil or if underplanted with black locust *(Robinia pseudoacacia)*. In two 10-year-old southern Illinois plantations, walnut trees in mixture with autumn-olive *(Elaeagnus umbellata)*, a nitrogen-fixing species, were 89 percent taller and 104 percent larger in diameter than walnut trees in pure walnut plots *(41)*. In an Indiana study, 10 years after autumn-olive was interplanted into 2-year-old black walnut, the walnut in the interplanted plots were 2.6 m (8.4 ft) taller than those in the pure plots *(14)*.

Mature black walnut trees on good sites may reach 30 to 37 m (100 to 120 ft) in height and 76 to 102 cm (30 to 40 in) in d.b.h. *(28)*. Trees 40 m (130 ft) tall and more than 244 cm (96 in) in d.b.h. have been reported in Wisconsin. In Indiana, black walnut trees were 46 m (150 ft) tall and 183 cm (72 in) in d.b.h. on the most favorable sites *(43)*. Research and experience indicate that with proper care it may be possible to produce 41-cm (16-in) saw logs in 30 to 35 years, and by planting on good sites it may be possible to produce 51 cm (20 in) veneer logs in 40 to 50 years. By applying some basic cultural practices, such as release and pruning, to established trees, growth and quality can be greatly increased in only a few years.

Board-foot volume growth rate was correlated with site quality in midwestern plantations. According to Kellogg's yield tables *(23)*, predicted yield for site index 21.3 m (70 ft) at age 75 is 10 times that of site index 12.2 m (40 ft), and yields for site index 18.3 m (60 ft) are twice those for site index 15.2 m (50 ft). The yield tables also show that periodic annual growth rate is not constant: maximum growth occurs between ages 40 and 50 years on the better sites.

Rooting Habit—The root system of mature black walnut has been described as combining the deep taproot of more xeric trees, such as the oaks, with the strong laterals characteristic of more mesic ones, such as maple. The rooting configuration of individual trees depends on soil texture and moisture conditions *(47)*.

The root system is deep and wide spreading, with a definite taproot, at least in early life. The taproot of a 9-year-old walnut tree excavated from an Indiana plantation was 2.3 m (7.5 ft) long and the lateral roots extended more than 2.4 m (8 ft) from the taproot *(11)*. One-year-old walnut seedlings lifted from nursery seedbeds have well-developed taproots *(51)*. The mass of fibrous roots varies with the soil type; the more fibrous-rooted seedlings develop in the more sandy-textured soils.

Early growth of the seedling root system is rapid. Vertical taproot extension during the first growing season is great, especially on drier soils. One researcher reported a taproot penetration of more than 1.2 m (4 ft) for 1-year-old walnut seedlings on a prairie silt loam soil. Another reported 64 to 69 cm (25 to 27 in) for 1-year-old walnut on a more moist site *(47)*. In the second year of root growth, the taproot continues to extend and many lateral roots develop.

The depth of walnut lateral roots may vary in response to root competition with its associates. In one study, lateral roots of walnut occupied a much shallower position in pure walnut stands than in mixed walnut-ash stands. This was explained by theorizing that the ash, having a strongly developed surface root system, forced the walnut roots into deeper soil layers. Root competition with Norway maple *(Acer platanoides)*, on the other hand, was not as intense *(47)*.

Black walnut is moderately tolerant of flooding. Mature trees are generally killed after 90 days of continuous inundation during the growing season, although some individuals may survive for 150 days or more. Black walnut is more flood-tolerant than black cherry, shortleaf pine *(Pinus echinata)*, basswood, and shagbark hickory *(Carya ovata) (47)*.

The initial root form of black walnut, with its rapidly growing juvenile taproot and wide spreading laterals, is characteristic of species that grow on deep, fine-textured soils in regions with well-distributed summer rains. Such soils maintain a fairly uniform available water content to considerable depth, and walnut growing on these soils are able to draw their moisture and nutrients largely from the more fertile shallow soil while still being able to rely on the deeper soil layers for survival during times of drought.

Black walnut forms endomycorrhizae of the vesicular-arbuscular type. One study revealed that 100 percent of the walnut seedlings grown in a southern Michigan nursery had endomycorrhizae, but seedlings grown in a southern Indiana nursery had no mycorrhizae. A recent study shows that several Glomus species form a symbiotic relation with black walnut seedlings. Some Glomus species and combinations of species increased growth of black walnut *(36)*.

Reaction to Competition—Black walnut is classed as intolerant of shade *(2)*. In mixed forest stands it must be dominant or codominant to survive, although it has survived and grown in the light shade of black locust. In a mixed hardwood stand in Indiana, pole-size black walnut responded to crown release by more than doubling diameter growth over a 10-year period *(39,40)*. Trees only partially released grew about 50 percent more than unreleased trees. Controlling understory growth had little effect on growth of the walnut trees. Following release, dominant and codominant trees continue to grow more rapidly than those in intermediate or suppressed crown classes, but strong intermediates often respond most to release (in terms of growth rate increase). A walnut tree should be considered for release if it is healthy, has a bole with potential to make a veneer or high quality saw log, and is small enough that it can reasonably be left for at least 10 more years. To be effective, release must be thorough. A rule of thumb is that at least three-fourths of the crown of the released tree should be at least 1.5 m (5 ft) from the crowns of adjacent trees 60 to 100 percent as tall, and at least 3 m (10 ft) from the crowns of taller trees. Subsequent releases will be required at intervals of 6 to 10 years to maintain free growing space.

Some bole sprouting can be expected on forest-grown trees that are released for the first time. Bole sprouts developed on almost half of the unreleased trees and on almost two-thirds of the released trees during an Indiana study *(39)*. Sprouts were more numerous on the unreleased trees (16.1 sprouts per tree) than on the partially (12.2 sprouts per tree) and completely released trees (9.2 sprouts per tree), but the sprouts were much larger on the released trees. The intermediate and suppressed trees had more sprouts than dominant or codominate trees. Most of the bole sprouts were above the butt log, and more were on the south side than on the north side of the trees.

Control of competing vegetation is especially important in new plantations. In an Indiana study, walnut seedlings established on formerly cultivated fields and given 3 years of weed control were 100 cm (39 in) taller at 10 years of age, and 15 mm (0.6 in) larger d.b.h. than trees given 2 years of control *(53)*. Trees with vegetation controlled 2 years were 40 cm (15.7 in) taller and 5 mm (0.2 in) larger in diameter than those where weeds were controlled only 1 year. Broadcast weed control is neither necessary nor desirable because it aggravates erosion problems.

In a southern Illinois experiment, seventh-year survival of black walnut planted on a cleared forest site was 94 to 99 percent regardless of weed control treatment *(25)*. The young trees grew better, however, when all vegetation or only forbs and grasses were controlled than when only woody vegetation was controlled or when no vegetation control was used. Biennial control was no better than triennial, but annual control was superior. When only woody vegetation was controlled, frequency of treatment had no effect.

Pruning lateral branches helps to produce knot-free wood under open growing conditions that would normally permit most of the lower branches to persist. The objective of pruning is to produce a clear bole while minimizing damage to the tree and growth loss. When needed, pruning should be begun early in the life of the tree and continued as needed. To minimize damage and promote rapid healing, branches should be pruned before they are 5 cm (2 in) d.b.h. A neat, clean cut should be made, being careful not to be cut into the branch collar *(44)*. Ring shakes and dark bands of discolored wood were associated with 14 of 17 stubs that were "flush cut" (branch collar removed) 13 years earlier. Pruning young trees eliminates these problems, but if older trees are pruned, care must be taken not to remove the branch collars that form around the bases of dying and dead branches.

When trees are pruned during the dormant season (early spring just before the leaves appear is best), wounds tend to heal more rapidly and completely and sprouts from dormant buds near the wound are less likely to develop. If sprouts do develop, they should be removed promptly. No more than 25 percent of the live crown should be released in a single year, and at least 50 percent of the total tree height should be maintained in live crown *(10)*.

Damaging Agents—Black walnut is damaged by a number of insects. In southern Illinois more than 300 insect species were found on black walnut *(49)*. Even though many insects feed on black walnut, only a few are considered serious pests. Two of the most common defoliating insects are the walnut caterpillar *(Datana integerrima)* and the fall webworm *(Hyphantria cunea)*. They are commonly found eating the leaves beginning in midsummer and continuing until September. Important boring insects are the ambrosia beetle *(Xylosandrus germanus)*, which may introduce a *Fusarium* fungus into the tree, causing dieback and resprouting from the base of the tree; the flat-headed apple tree borer *(Chrysobothris femorata)*, which feeds in the phloem and outer sapwood area as larvae and on the foliage as adults; the walnut curculio *(Conotrachelus retentus)*, which damages developing nuts when the larvae bore into them and cause great losses during the so-called "June drop" of walnuts; and the walnut shoot moth *(Acrobasis demotella)*, which damages the terminal buds in early spring when the larvae bore into the still unexpanded bud, causing multiple forks and crooks in the main stem. The pecan leaf casebearer (*Acrobasis juglandis*) is closely related to the walnut shoot moth but is a much less damaging pest of black walnut. Important sucking insects are aphids or plant lice (*Monellia* spp. and *Monelliopsis* spp.), which suck the juices from leaves and often deposit a sticky substance called "honey-dew" on the leaf surface that may turn black and prevent photosynthesis; and the walnut lace bug (*Corythucha juglandis*), which causes damage when the adults and nymphs suck the sap from the lower surfaces of walnut leaflets.

Black walnut is susceptible to only a few serious diseases, but their impact is significant. Two serious root rot diseases found in seedling nurseries are caused by the fungi *Phytophthora citricola* and *Cylindrocladium* spp. An important mold of stored seed and seedlings is associated with *Penicillia* and other normally saprophytic fungi (*24*). Walnut anthracnose, caused by the fungus *Gnomonia leptostyla*, is a leaf spot disease that begins during wet spring weather, although symptoms may not become visible until June or July (*49*). Another important foliage disease is target leafspot which is caused by the fungus *Cristulariella pryamidalis* and is responsible for premature defoliation (*38*). A newly discovered, serious leaf spot disease is caused by the fungus *Mycosphaerella juglandis* (*24*).

Important stem diseases caused by fungi are the *Fusarium* cankers caused by several species of *Fusarium* and the perennial target canker (*Nectria galligena*) commonly known as Nectria canker (*49*). Cankers usually occur on the main stem where a branch broke off and left an open wound.

Animals damage black walnut in several ways. Deer browse on buds and rub antlers against young trees. Mice and rabbits gnaw on the stems of young trees during the winter, and squirrels dig up and eat direct-seeded nuts and feed on green and mature nuts still on the trees. Perching birds break the terminal or new branches from the tree, and the yellow-bellied sapsucker drills holes through the bark during late winter or early spring (*49*). Some trees may be nearly girdled with peck holes.

Decay, dieback, and frost also cause damage. At times dieback and frost damage may be extensive. Late spring frosts kill succulent new growth and thus reduce height growth and destroy desirable form. Late winter warming periods sometimes cause walnut trees to break dormancy prematurely, resulting in freezing injury to the stem tissue (*13,37*).

Special Uses

The best known use of black walnut is for its lumber and veneer. The wood is used for fine furniture of all kinds, interior paneling, specialty products, and gunstocks.

The nuts of black walnut serve many purposes. The kernels provide food for wildlife and humans (*45,52*). Ground shells provide special products (*12*). During World War II, airplane pistons were cleaned with a "nut shell" blaster and this idea was carried into the auto industry; manufacturers used shells to deburr precision gears. Ground shell products are also used to clean jet engines, as additives to drilling mud for oil drilling operations, as filler in dynamite, as a nonslip agent in automobile tires, as an air-pressured propellant to strip paints, as a filter agent for scrubbers in smokestacks, and as a flourlike carrying agent in various insecticides.

Genetics

Population Differences

Black walnut contains great genetic variation for growth and survival, and an important part of this variation is related to geographic origin (*8*). Preliminary seed collection zones have been recommended (*15*). Geographic variation among stands is three to five times greater than local (within stands) variation for characteristics such as growth rate, dates of foliation and leaf drop, twig maturation, and degree of winter dieback (*17*). Genetic gains can be made through selection within a designated seed collection zone. Generally, trees from seed collected south of the planting site grow as fast or faster in height and diameter than trees from local or northern sources (*7,9*). Both duration and rate of growth are responsible for the growth differences. In 1969, trees from Mississippi and Texas seed sources planted in a southern Illinois plantation grew in height for 134 days compared to [illegible] days for trees from northern Illinois and Iowa sources (*5*). On the average, height growth continued 1 day longer for every 24 miles south of the planting site that seed was collected (*6*). Duration of diameter growth was less closely related. However, trees of southern origin grew fastest.

Flowering phenology, seed weight, kernel percent, nut crackability, foliage characteristics, grafting and budding compatibility, rooting capacity of layered trees in stool beds, autumn leaf retention, cold resistance, and growth rates vary widely among black walnut families (*17*).

More than 400 black walnut cultivars have been named and released during the past century. Twenty of the most popular, including origin and nut evaluations, are listed by Funk (*18*). Three timber-type walnut clones chosen for outstanding straightness, anthracnose resistance, or late spring foliation have been patented by Purdue University.

Hybrids

Wright *(54)* has pointed out that species that can cross within a genus usually have distinct (often adjacent) ranges, while species that occupy the same sites in the same regions develop barriers to hybridization. *Juglans* seems to follow this pattern; *J. nigra* and *J. cinerea* often grow together but apparently never cross naturally, while all other walnut species (at least in the western hemisphere) are almost completely isolated. Thus, easy crossing might be expected among the morphologically similar North America Rhysocaryon walnuts. One example is the "Royal" hybrid between *J. nigra* and *J. hindsii* produced by Burbank in about 1888. This hybrid begins to bear viable seed by age 5 and produces exceptionally large nuts *(50)*. The hybrids are vigorous and have been recommended for timber areas. Black walnut has been crossed with other species of *Juglans* in attempts to increase nut production, to produce a thin-shelled nut, or to produce a faster growing tree. *Juglans* can be divided into three sections: the black walnuts, the butternuts, and the Persian/Carpathians. A somatic chromosome number of 32 is consistent for all the species reported to date *(18)*.

Crossing between the black walnut and butternut sections is difficult or impossible. A cross between *J. nigra* and *J. ailantifolia* is the only one recognized between the black walnut and butternut sections. However, *J. regia* can hybridize with species in both the other sections, although the crosses are not always easy.

Artificial hybridization is simple but time consuming. Each pollination may yield two or three nuts and a season's work only a few thousand nuts.

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Liquidambar styraciflua L. Sweetgum

Hamamelidaceae Witch-hazel family

Paul P. Kormanik

Sweetgum (*Liquidambar styraciflua*), also called redgum, sapgum, starleaf-gum, or bilsted, is a common bottom-land species of the South where it grows biggest and is most abundant in the lower Mississippi Valley. This moderate to rapidly growing tree often pioneers in old fields and logged areas in the uplands and Coastal Plain and may develop in a nearly pure stand. Sweetgum is one of the most important commercial hardwoods in the Southeast and the handsome hard wood is put to a great many uses, one of which is veneer for plywood. The small seeds are eaten by birds, squirrels, and chipmunks. It is sometimes used as a shade tree.

Habitat

Native Range

Sweetgum (fig. 1) grows from Connecticut southward throughout the East to central Florida and eastern Texas. It is found as far west as Missouri, Arkansas, and Oklahoma and north to southern Illinois. It also grows in scattered locations in northwestern and central Mexico, Guatemala, Belize, Salvador, Honduras, and Nicaragua.

Climate

Annual rainfall varies from 1020 mm (40 in) in the North to 1520 mm (60 in) in the South; the growing season rainfall is 510 to 610 mm (20 to 24 in). There are 180 frost-free days in the northern part of its range and up to 320 in the southern part. January temperatures are less than -1° C (30° F) in the North and about 10° C (50° F) in the South; minimum temperatures during the year are -21° C (-5° F) in the North and -4° C (25° F) in the South. Maximum temperature during the year is about 38° C (100° F) for most of the range of sweetgum.

Soils and Topography

Sweetgum is perhaps one of the most adaptable hardwood species in its tolerance to different soil and site conditions. As is characteristic of most hardwood species, it grows best on the moist alluvial clay and loamy soils of river bottoms, but its growth rate is commercially acceptable on a wide range of Piedmont and Coastal Plain soils.

Throughout the Piedmont Plateau, sweetgum makes good growth on the river and stream bottoms and shows considerable potential on many upland sites. In the Carolina and Georgia Piedmont, for example, it is exceptionally competitive with other tree species on a wide range of soils with a site index for loblolly pine of 75 (at age 50) or greater.

In Maryland, sweetgum rarely makes acceptable growth on clay or gravelly clay upland soils and is rarely found on well-drained, sandy soils. Best growth rates are obtained on alluvial swamp sites and on imperfectly and poorly drained soils having a high clay content.

In the lower Mississippi Valley, site quality for sweetgum increases with the amount of exchangeable potassium in the soil and decreases as clay percentage increases. The best sites are those with medium-textured soils without a hardpan in the top 61 cm (24 in) and with moderate to good internal drainage. In the Mississippi Delta, sweetgum (fig. 2) is most common on silty clay or silty clay loam ridges and silty clay flats in the first bottoms, which are very moist, but not too poorly drained. Along the eastern border of the Mississippi River, sweetgum is occasionally dominant on the loessial soils of the alluvial flood plain. It is characteristically dominant on the relatively impervious Alfisols of the Illinoian till plain, including the very poorly drained Avonburg, Blanchester, and Clermont silt loams (*16*).

Associated Forest Cover

Sweetgum is a major component of four forest cover types (*6*): Pin Oak–Sweetgum (Society of American Foresters Type 65), Sweetgum–Willow Oak (Type 92), Sycamore–Sweetgum–American Elm (Type 94), and Sweetgum–Yellow-Poplar (Type 87). It is a minor component of at least 20 other cover types including Chestnut Oak (Type 44), White Oak–Black Oak–Northern Red Oak (Type 52), Black Oak (Type 110), Yellow-Poplar (Type 57), River Birch–Sycamore (Type 61), Silver Maple–American Elm (Type 62), Sassafras–Persimmon (Type 64), Longleaf Pine (Type70), Longleaf Pine–Slash Pine (Type 83), Shortleaf Pine (Type 75), Virginia Pine (Type 79), Loblolly Pine (Type 81), Loblolly Pine–Shortleaf Pine (Type 80), Pond Pine (Type 98), Willow Oak–Water Oak–Diamondleaf Oak (Type 88), Sugarberry–American Elm–Green Ash (Type 93), Baldcypress–

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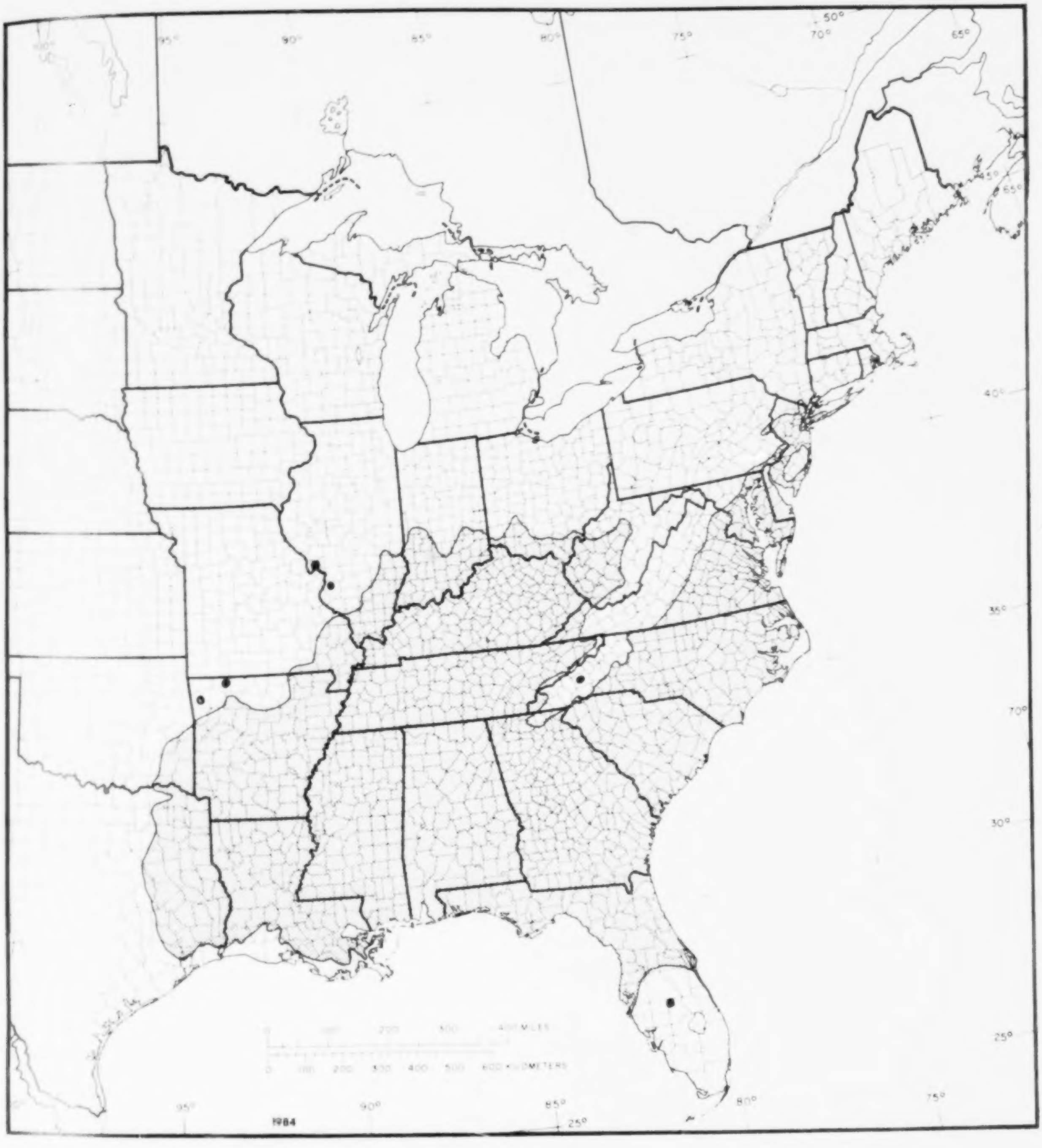
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Figure 1—*The native range of sweetgum.*

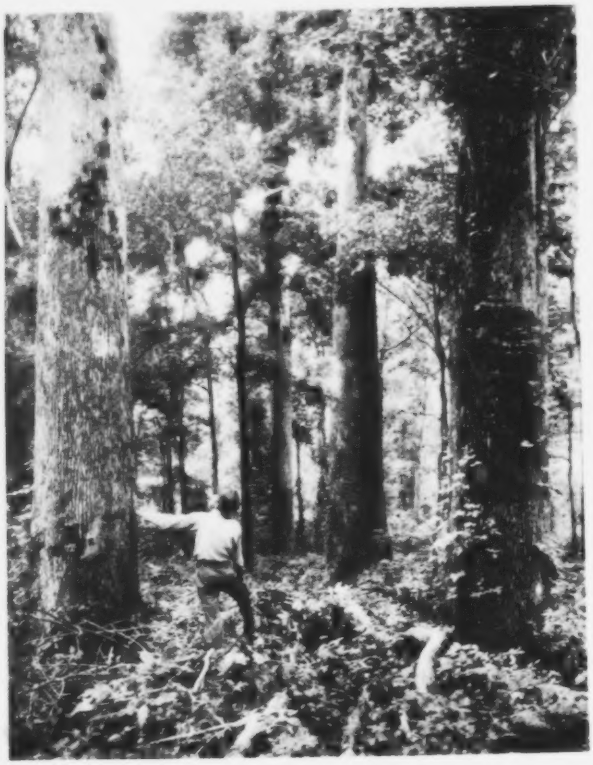

Figure 2—*Virgin sweetgum in the Mississippi bottom lands.*

Tupelo (Type 102), Water Tupelo–Swamp Tupelo (Type 103), Sweetbay–Swamp Tupelo–Redbay (Type 104), and Cabbage Palmetto (Type 74).

Among the most common associated tree species are red maple (*Acer rubrum*), boxelder (*A. negundo*), river birch (*Betula nigra*), pignut, shellbark, shagbark, and mockernut hickories (*Carya glabra, C. laciniosa, C. ovata, C. tomentosa*), sugarberry (*Celtis laevigata*), shortleaf pine (*Pinus echinata*), and loblolly pine (*P. taeda*). Several species of dogwood (*Cornus*) and alder (*Alnus*), as well as eastern redbud (*Cercis canadensis*), commonly occur as understory species with sweetgum.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sweetgum is monoecious. The small, greenish flowers bloom from March to early May, depending on latitude and weather conditions. Both the staminate and pistillate flowers occur in heads. The staminate inflorescences are racemes; the solitary pistillate flowers are globose heads that form the multiple heads, 2.5 to 3.8 cm (1 to 1.5 in) in diameter, of small, two-celled capsules. The lustrous green color of the fruiting heads fades to yellow as maturity is reached in September to November. The beaklike capsules open at this time, and the small winged seeds, one or two per capsule, are then readily disseminated by wind. However, the seed balls can be safely collected for seed extraction several weeks before ball discoloration occurs without harming the seed. Empty fruiting heads often remain on the trees over winter. Fair seed crops occur every year and bumper crops about every 3 years. The staminate and pistillate flowers are quite sensitive to cold and are often damaged by frost (*17*).

Seed Production and Dissemination—Trees begin to produce seeds when 20 to 30 years old and continue production until at least 150 years of age. Seed production varies widely depending on climatic conditions during the growing season. Under optimum conditions, seed balls may average as many as 56 sound seeds per ball, or as few as 7 or 8 under less favorable conditions (*16,17*). Seed balls have been collected for more than 12 years at the Forestry Sciences Laboratory, Athens, GA, and scientists there expect 20 to 30 sound seeds per ball in an average year but have found as few as 5 per ball in a bad year. Low percentages of sound seed appear to be correlated with prolonged summer drought and excessive soil moisture stress during the growing season in northeast Georgia.

There are approximately 365 g (0.8 lb) of clean seeds per 35 liters (1 bushel) of balls, and the number of seeds per 454 g (1 lb) varies from 65,000 to 98,400, with an average of 82,000 (*17*). Seed soundness may reach 80 to 90 percent in a good seed year but may drop to 10 to 20 percent in a bad seed year. There are no data relating to the number of sound seed required for normal seed-ball development. The maximum distance of seed dispersal recorded is 183 m (600 ft), but ordinarily 96 percent of the seed falls within 61 m (200 ft) of the point of release (*16*).

Seedling Development—Germination is epigeal (*17*). Some sod covers are not a serious hindrance to seed germination but can seriously affect seedling survival during seasons of below-average rainfall. Fescue, however, has been shown to have adverse allelopathic effects on sweetgum (*19*). From 40 to 60 percent first-year mortality was observed on sweetgum plots overseeded with fescue in a South Carolina Piedmont site (*3*). The mortality at the South Carolina site was due directly to competition and was not an allelopathic response.

Vegetative Reproduction—Few data are available on the early development of natural stands of sweetgum throughout its broad range. The limited, earlier data *(16)* indicate that workers were not aware of the tendency of sweetgum to regenerate from root sprouts that originated from suppressed root buds *(11)*. Stand disturbances thought to produce ideal seedbed conditions were actually optimum conditions for suppressed bud release and subsequent root sprout development. A South Carolina Coastal Plain area thought to have been successfully regenerated with sweetgum seed trees was later found to be regenerated primarily from root sprouts *(4,7,11)*.

The importance of root sprout formation with sweetgum regeneration is evident from observations made in natural stands of mixed pines and hardwoods in the Georgia Piedmont that have been logged for sawtimber. In most of the stands examined, advance reproduction of sweetgum was clearly evident, accounting for 10 to 60 percent of all hardwood production. The invasion of such stands by young sweetgum has usually been attributed to natural seeding, but most of the young, vigorously growing stems observed in the Georgia Piedmont were of sprout origin. It is not uncommon to find as many as 40 or more stems from seedling to sapling size on the root systems of a single parent tree. Additional work with root sprouts in the Coastal Plain of South Carolina showed that sprout height after 8 years was directly correlated with the diameter of the lateral root from which the sprout originated; the larger the root the taller the sprout.

The persistence of root sprouts was revealed when soil was removed from several 0.04-ha (0.1-acre) plots on a Georgia Piedmont bottom-land site that supported pure stands of sweetgum. Trees ranged in d.b.h. from about 25 to 41 cm (10 to 16 in) and varied from dominant to intermediate in the crown canopy. More than 70 percent of the trees were of sprout origin on most plots. Other stands that were primarily of seed origin were later found on abandoned agricultural lands. These observations indicate that a significant portion of sweetgum regeneration following logging can be expected to originate from root sprouts. The long-term development and management of these stands have yet to be clarified.

Plantation establishment of sweetgum is becoming increasingly important throughout the southern region, and it is rapidly becoming the hardwood species most commonly established. Results of early plantation establishment and development have been quite variable. This variability in growth has been attributed to seedling quality. Seedlings with a large root-collar diameter achieve the best growth, and planting seedlings with a root-collar diameter of less than 6 mm (0.25 in) is not recommended *(2)*. In a Georgia Piedmont bottom-land site, seedlings at age 7 ranged in height from 3.8 to 6.2 m (12.4 to 20.2 ft). After 7 years on a strip mine in Indiana, sweetgum averaged 2.1 m (7 ft). On favorable sites in the lower Mississippi Valley, seedling height growth of 0.6 m/yr (2 ft/yr) has been reported. On upland sites, 5-year height growth varies considerably, from 1.1 m (3.6 ft) on an eroded field to 2.0 m (6.5 ft) on areas reverting to woody cover. It is this slow, early growth of sweetgum plantations that is of concern to silviculturists because it necessitates expensive cultivation to reduce weed competition and thereby maintain acceptable survival until height growth begins. First-order lateral root morphology of nursery-lifted sweetgum seedlings reflects their future competitiveness in the field. Early growth and survival can be acceptable, even in moderate to severe drought years, if nursery-lifted seedlings have five or more first-order lateral roots exceeding 1 mm (0.04 in) in diameter at the junction with the taproot. As many as one third of all seedlings in selected families growing in one nursery did not meet these standards making them poorly competitive in a forest environment *(10)*.

Recent work suggests that vesicular-arbuscular mycorrhizae can significantly improve seedling quality from nurseries *(9,13,14)* and alter this pattern of low growth so commonly encountered during the first 3- to 5-year period following plantation establishment. On an upland Piedmont site in South Carolina, for example, total heights on sweetgum plots after three growing seasons have been observed to exceed the 2.0 m (6.5 ft) reported after five growing seasons from areas just reverting to woody cover. On a denuded borrow pit in the South Carolina Piedmont, soil amended with as little as 13 mm (0.5 in) of sewage sludge evenly distributed and disked into the soil resulted in fourth-year height of 2.8 m (9.2 ft) for sweetgum *(3)*. The seedlings used in this experiment were heavily mycorrhizal with a vesicular-arbuscular fungus *(Glomus mosseae)* at outplanting.

Sapling and Pole Stages to Maturity

Growth and Yield—Young sweetgum have a strong excurrent growth habit and long, conical crowns that usually prune themselves readily under forest conditions. There is a wide range in branch angle from acute to almost 90° in young trees. Depending on site quality, and at a definite stage in development, sweetgum becomes decurrent as the trees mature, and the crown becomes rounded and wide spreading. The tops of overmature trees are usually broken or stag headed.

The excurrent growth habit is maintained longer on the more moist, fertile bottom-land sites than on the drier, less fertile upland sites. However, on excessively dry sites the excurrent growth habit is characteristically maintained for many years and may represent a morphological growth response mediated by moisture availability.

The average 10-year diameter growth for overmature sweetgum in the southern region was reported to be 4.8 cm (1.9 in), and for immature trees of medium to high vigor, 8.9 cm (3.5 in) *(16)*. In the Mississippi Delta, pure stands of sweetgum average 84 to 112 m^3/ha (6,000 to 8,000 fbm/acre). Very good stands have 210 to 280 m^3/ha (15,000 to 20,000 fbm/acre) with up to 420 to 560 m^3/ha (30,000 to 40,000 fbm/acre) on small, selected areas. On ridges and upland sites, stands are usually less dense than on bottom-land sites.

Rooting Habit—Early root development varies with site conditions. On well-drained bottom-land sites a deep taproot with numerous well-developed laterals usually develops rapidly. On wet sites with poor drainage, however, the root system is shallow and wide spreading, with little tendency shown for taproot development. On gravelly ridges, hillsides, and upland piedmont sites, sweetgum develops a particularly strong taproot and is very resistant to wind *(16)*.

Reaction to Competition—Sweetgum is most accurately classed as intolerant of shade. It must have adequate sunlight to reach its potential. Young sweetgum are able to endure some crowding in pure stands on bottom lands. With increasing age, however, they become less able to endure competition and may respond poorly to release because crown regeneration capacity is reduced. Sweetgum of all vigor classes tend to develop epicormic branches when stands are thinned excessively. Moderate thinnings stimulate epicormic branches, primarily on trees with light to moderate crown development *(12)*. On upland sites in the southern and southeastern regions, sweetgum seedlings or sprouts are often present in the pine forest understory. Removal of the pine overstory usually results in rapid growth of the sweetgum. This response may be attributed to logging damage to the original understory stems, which then resprout and grow rapidly without overhead competition.

Damaging Agents—Few severe diseases are associated with sweetgum, but small mammals and grazing animals have caused isolated problems. Seedlings may be badly damaged by hogs, goats, or cattle in different areas. Rodents, particularly mice, and rabbits have caused considerable damage to young plantations in several areas *(16)*. Beavers in the Georgia Piedmont cause impoundments and girdle healthy trees.

Fire may be one of the major agents of damage to this species. Summer fires damage young sweetgum more than winter fires. Fire scars on living trees furnish entrance points for both insects and diseases. As long as the sapwood is not killed by fire, basal wounds are often covered with a gum exudation that protects them. With repeated fires, however, the tree is apt to have some sapwood killed, and fungi and insects may become established. In the lower delta of the Mississippi River, 42 percent of the sweetgum trees burned once showed decay 8 years later; 79 percent of the trees burned repeatedly during an 8-year period showed decay *(16)*.

The four most common decay organisms reported in the Mississippi River Delta were *Fomes geotropus*, *Pleurotus ostreatus*, *Lentinus trigrinus*, and *Ganoderma lucidum* *(16)*.

Other diseases of sweetgum that may be important occasionally are an abiotic leader dieback or blight, twig canker, and trunk lesion caused by *Botryosphaeria ribis*, and bleeding necrosis, which may be a combination of sweetgum blight and *B. ribis* trunk lesion *(8)*. Of these, only sweetgum blight is widely distributed and has caused heavy mortality in several States. It has received intensive study in Maryland and Mississippi. Drought appears to be the primary cause. In the lower Mississippi River flood plain, blight severity was found to be correlated with soil properties affecting moisture supply. Severity of dieback was reduced by 68 percent in 2 years by irrigating when soil moisture dropped below 40 percent of field capacity *(16)*. There is a good possibility that sweetgum blight is most common in stands of root sprout origin. In the Georgia Piedmont and Coastal Plain of South Carolina, many groups of trees are composed of stems that are of root sprout origin and depend on a single root system complex for water uptake. During prolonged droughts such as occurred in the 1950's, this limited root system may not be adequate to satisfy the water requirements of the sprout complex, and many of the stressed trees may suffer blight.

Except for leaffeeders, insects usually attack only trees that are already damaged, decadent, or dead. These include the bark beetles *(Dryocoetes betulae* and *Pityophthorus liquidambarus)*, the ambrosia beetles, which include *Platypus compositus*, and the darkling beetles *(Strongylium* spp.). The leaffeeders include the forest tent caterpillar *(Malacosoma disstria)* and the luna moth *(Actias luna)* *(1)*. In addition, a treehopper *(Strictocephala militaris)* is known to spend its entire life cycle on sweetgum in northeast Georgia but is not considered to be harmful *(5)*.

Special Uses

Sweetgum is used principally for lumber, veneer, plywood, slack cooperage, railroad ties, fuel, and pulpwood. The lumber is made into boxes and crates, furniture, radio-, television-, and phonograph cabinets, interior trim, and millwork. The veneer and plywood are used for boxes, pallets, crates, baskets, and interior woodwork *(18)*.

Genetics

No hybrids of sweetgum are known to exist. There is considerable evidence, however, that differences between ecotypes, such as swamps and uplands, should play an important role in selection of mother trees for artificial regeneration programs *(15)*.

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Liriodendron tulipifera L. Yellow-Poplar

Magnoliaceae Magnolia family

Donald E. Beck

Yellow-poplar (*Liriodendron tulipifera*), also called tuliptree, tulip-poplar, white-poplar, and whitewood, is one of the most attractive and tallest of eastern hardwoods. It is fast growing and may reach 300 years of age on deep, rich, well-drained soils of forest coves and lower mountain slopes. The wood has high commercial value because of its versatility and as a substitute for increasingly scarce softwoods in furniture and framing construction. Yellow-poplar is also valued as a honey tree, a source of wildlife food, and a shade tree for large areas.

Habitat

Native Range

Yellow-poplar (figs. 1, 2) grows throughout the Eastern United States from southern New England, west through southern Ontario and Michigan, south to Louisiana, then east to north–central Florida *(22)*. It is most abundant and reaches its largest size in the valley of the Ohio River and on the mountain slopes of North Carolina, Tennessee, Kentucky, and West Virginia. The Appalachian Mountains and adjacent Piedmont running south from Pennsylvania to Georgia contained 75 percent of all yellow-poplar growing stock in 1974.

Climate

Because of its wide geographic distribution, yellow-poplar grows under a variety of climatic conditions. Low temperature extremes vary from severe winters in southern New England and upper New York with a mean January temperature of -7.2° C (19° F) to almost frost-free winters in central Florida with a mean January temperature of 16.1° C (61° F). Average July temperature varies from 20.6° C (69° F) in the northern part of the range to 27.2° C (81° F) in the southern. Rainfall in the range of yellow-poplar varies from 760 mm (30 in) to more than 2030 mm (80 in) in some areas of the southern Appalachians. Average number of frost-free days varies from 150 to more than 310 days within the north-to-south range of yellow-poplar.

Effects of temperature and moisture extremes are tempered somewhat by local topography. At the northern end of its range, yellow-poplar is usually found in valleys and stream bottoms at elevations below 300 m (1,000 ft). In the southern Appalachians, it may grow on a variety of sites, including stream bottoms, coves, and moist slopes up to an elevation of about 1370 m (4,500 ft). Toward the southern limit of the range, where high temperatures and soil moisture probably become limiting, the species usually is confined to moist, but well-drained, stream bottoms. Optimum development of yellow-poplar occurs where rainfall is well distributed over a long growing season.

Soils and Topography

Yellow-poplar thrives on many soil types with various physical properties, chemical composition, and parent material. Within the major portion of the range of yellow-poplar, these soils fall in soil orders Inceptisols and Ultisols. Exceptionally good growth has been observed on alluvial soils bordering streams, on loam soils of mountain coves, on talus slopes below cliffs and bluffs, and on well-watered, gravelly soils. In general, where yellow-poplar grows naturally and well, the soils are moderately moist, well drained, and loose textured; it rarely does well in very wet or very dry situations.

Studies in locations as varied as the Coastal Plain of New Jersey, the Central States, the Great Appalachian Valley, the Carolina and Virginia Piedmonts, the Cumberland Plateau, and the mountains of north Georgia have isolated soil features that measure effective rooting depth and moisture-supplying capacity as the most important determinants of growth *(13, 18, 25, 30, 35)*. These variables have been expressed in quantitative terms such as relative content of sand, silt, and clay; depth of humus accumulation; organic matter content of different horizons of the soil profile; percent moisture retention; available water; and depth to impermeable layers.

The same studies also stressed that topographic features plus latitude and elevation, which partially determine the amount of incoming solar radiation and rate of evaporation or otherwise influence the moisture supplying capacity of soil, are important variables in assessing site suitability for yellow-poplar growth. The best growth usually occurs on north and east aspects, on lower slopes, in sheltered coves, and on gentle, concave slopes.

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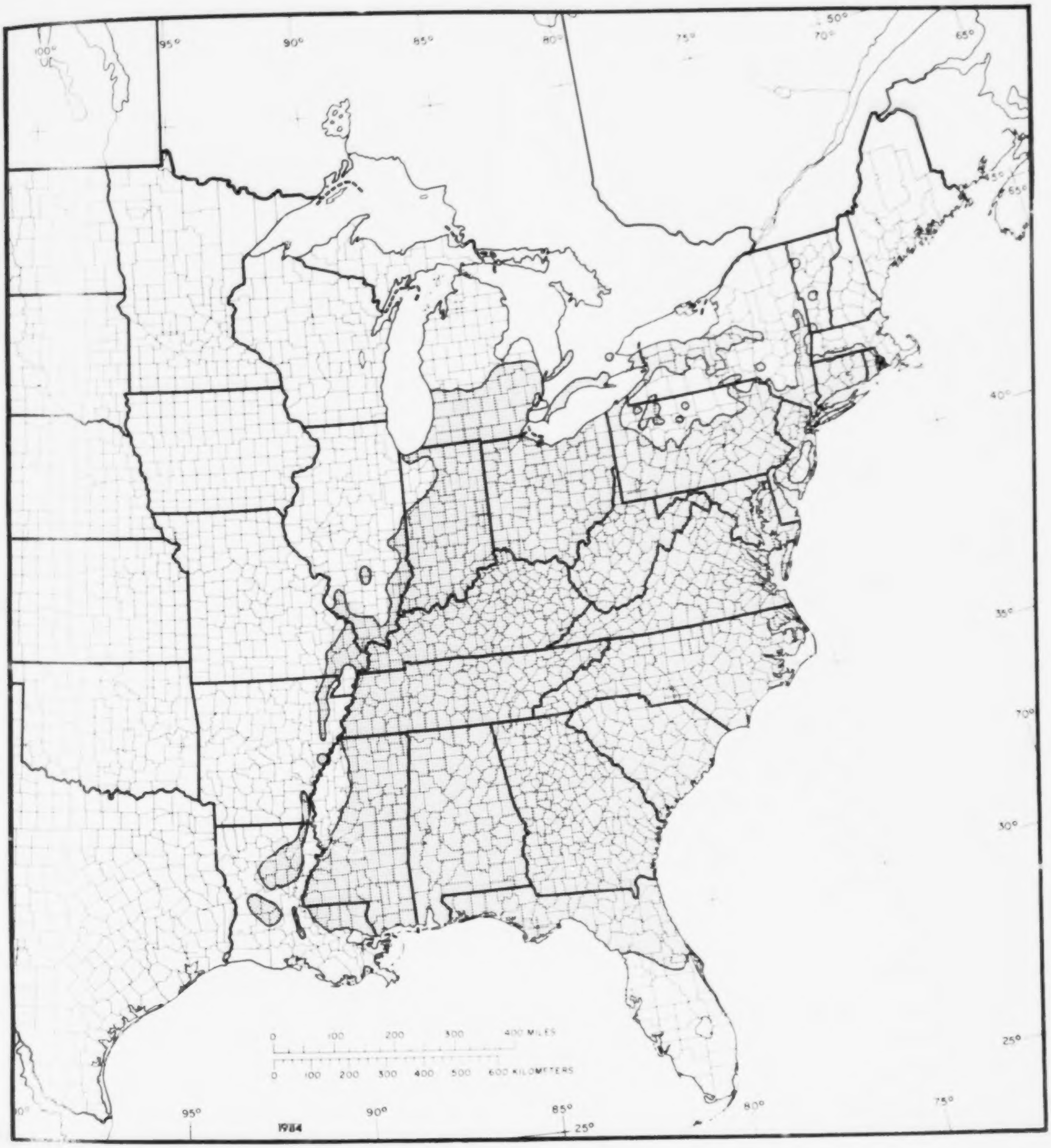
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Figure 1—*The native range of yellow-poplar.*

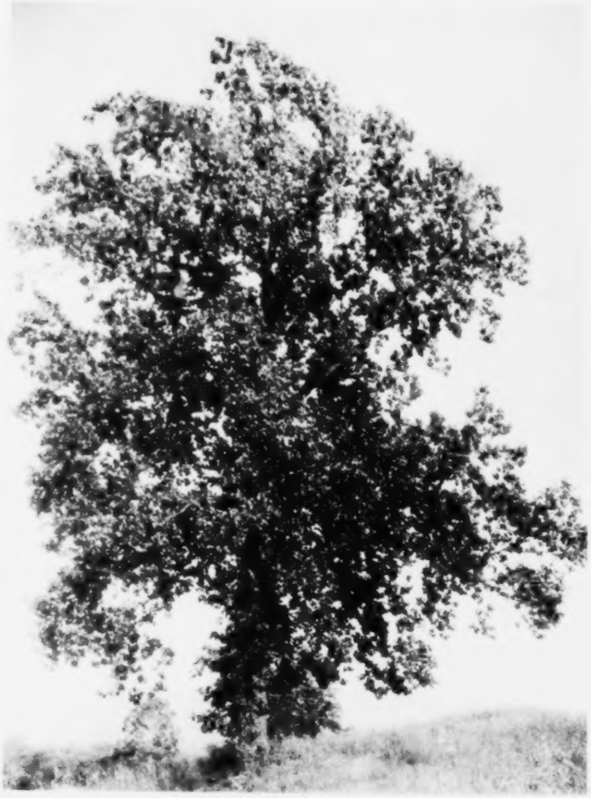

Figure 2—*Open-grown yellow-poplar.*

Low levels of soil nutrients—most frequently nitrogen—have occasionally been linked to slow rates of growth for yellow-poplar. Also, naturally occurring levels of phosphorous and potassium can limit growth. However, soil physical properties far overshadow chemical properties in determining distribution and growth of yellow-poplar.

Associated Forest Cover

Yellow-poplar is a major species in four forest cover types (Society of American Foresters) *(14)*: Yellow-Poplar (Type 57), Yellow-Poplar–Eastern Hemlock (Type 58), Yellow-Poplar–White Oak–Northern Red Oak (Type 59), and Sweetgum–Yellow-Poplar (Type 87). It is a minor species in 11 types: Eastern White Pine (Type 21), White Pine–Hemlock (Type 22), White Pine–Chestnut Oak (Type 51), White Oak–Black Oak–Northern Red Oak (Type 52), White Oak (Type 53), Northern Red Oak (Type 55), Beech–Sugar Maple (Type 60), Sassafras–Persimmon (Type 64), Loblolly Pine (Type 81), Loblolly Pine–Hardwood (Type 82), and Swamp Chestnut Oak–Cherrybark Oak (Type 91).

On bottom lands and on the better drained soils of the Coastal Plain, yellow-poplar grows in mixture with the tupelos *(Nyssa* spp.), baldcypress *(Taxodium distichum)*, oaks *(Quercus* spp.), red maple *(Acer rubrum)*, sweetgum *(Liquidambar styraciflua)*, and loblolly pine *(Pinus taeda)*. In the Piedmont, associated species include oaks, sweetgum, blackgum *(Nyssa sylvatica)*, red maple, loblolly pine, shortleaf pine *(Pinus echinata)*, Virginia pine *(P. virginiana)*, hickories *(Carya* spp.), flowering dogwood *(Cornus florida)*, sourwood *(Oxydendrum arboreum)*, and redcedar *(Juniperus virginiana)*.

At lower elevations in the Appalachian Mountains, yellow-poplar (fig. 3) is found with black locust *(Robinia pseudoacacia)*, white pine *(Pinus strobus)*, eastern hemlock *(Tsuga canadensis)*, hickories, white oak *(Quercus alba)*, other oaks, black walnut *(Juglans nigra)*, yellow pines, flowering dogwood, sourwood, sweet birch *(Betula lenta)*, blackgum, basswood *(Tilia americana)*, and Carolina silverbell *(Halesia carolina)*. At higher elevations, associated species include northern red oak *(Quercus rubra)*, white ash *(Fraxinus americana)*, black cherry *(Prunus serotina)*, cucumber tree *(Magnolia acuminata)*, yellow buckeye *(Aesculus octandra)*, American beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum)*, and yellow birch *(Betula alleghaniensis)*. Trees associated with yellow-poplar in nonmountainous areas of the North and Midwest include white oak, black oak *(Quercus velutina)*, northern red oak, ash, beech, sugar maple, blackgum, dogwood, and hickories.

Pure stands of yellow-poplar occupy only a small percentage of the total land within the range of the species, but they are usually on productive sites that include some of the most valuable timber-producing forests in eastern North America. It has been repeatedly observed in the southern Appalachians that the percentage of yellow-poplar increases noticeably with increasing quality of the site. Where yellow-poplar grows in pure, or nearly pure, stands on medium and lower quality sites, it probably originated on abandoned old fields.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yellow-poplar has a singly occurring, perfect flower 4 to 5 cm wide (1.5 to 2 in), with six petals varying in color from a light yellowish green at the margin to a deep orange band

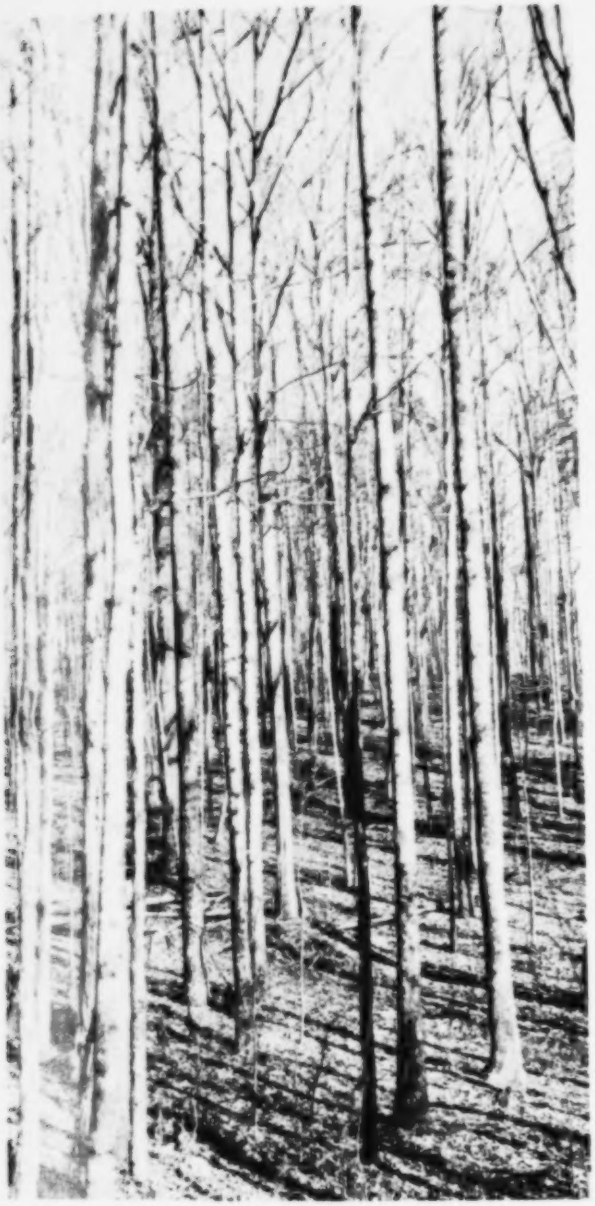

Figure 3—Even-aged stand of yellow-poplar with some hickory on Nantahala National Forest, NC.

at the center. Yellow-poplars usually produce their first flowers at 15 to 20 years of age and may continue production for 200 years *(29,31)*. Flowering occurs from April to June depending on location and weather conditions. The flowering period for each tree varies from 2 to 6 weeks depending on the size and age of the tree and number of flowers per tree. Pollination must occur soon after the flowers open while the stigmas are light colored and succulent; brown stigmas are no longer receptive to pollen. Normally the receptive period is only 12 to 24 daylight hours. Insects are important pollinators; flies, beetles, honey bees, and bumble bees (in decreasing order of abundance) were observed on opened flowers. However, uncontrolled insect pollinations do not result in effective pollination of all stigmas, and a great deal of selfing occurs *(7)*. Higher percentages of filled seed result from cross-pollination and crosses among widely separated trees *(37)*. By controlled cross-pollination, as many as 90-percent filled seed per cone was obtained; the highest percentage for an open-pollinated tree was 35 percent. Cross-pollinated seedlings tended to be more vigorous than seedlings obtained from open pollination.

Seed Production and Dissemination—The conelike aggregate of many winged carpels ripens and matures from early August in the North to late October in the South. In the Piedmont of North Carolina, seedfall begins in mid-October and reaches its peak early in November. High seedfall occurs during dry periods with high temperatures, while periods of heavy rainfall result in low seed dissemination rates. Viable seed is disseminated from mid-October to mid-March; the percentage of viability, which ranges from 5 to 20 percent, is about equal throughout the period.

Yellow-poplar is a prolific seeder, and large crops are produced almost annually *(29,31)*. In North Carolina, a 25-cm (10-in) tree produced 750 cones with 7,500 sound seeds, and a 51-cm (20-in) tree produced 3,250 cones with 29,000 sound seeds. A seedfall of 741,000 to 1,482,000/ha (300,000 to 600,000/acre) is not uncommon. Measurement of the 1966 seed crop in 19 southern Appalachian stands showed an average of 3.7 million seeds per hectare (1.5 million/acre). Seed size is highly variable, the number per kilogram ranging from 11,000 to 40,000 (5,000 to 18,000/lb). In general, southern seeds are larger than northern ones.

The individual, winged samaras may be scattered by the wind to distances equal to four or five times the height of a tree. In southern Indiana, a seedfall pattern was shown to be oval, with the center north of the seed tree. Prevailing south and southwest winds occasionally carried seeds more than 183 m (600 ft). Distribution of filled seeds occurred in satisfactory numbers—2,470 to 24,700/ha (1,000 to 10,000/acre)—as far as 60 m (200 ft) from a good seed tree in the direction of the prevailing wind and 30 m (100 ft) in all other directions.

Yellow-poplar seeds retain their viability in the forest floor from 4 to 7 years *(11)*. Large quantities of seeds in the forest floor are capable of producing seedlings when suitable environmental conditions exist. In West Virginia, a study in three 40-year-old stands with 101 to 470 yellow-poplar trees per hectare (41 to 190/acre) showed from 240,000 to 475,000 sound seeds per hectare (97,000 to 192,000/acre) in the forest floor *(17)*. These seeds produced between 138,000 to 190,000 seedlings per hectare (56,000 to 77,000/acre) when transferred to an open area and kept well watered.

Seedling Development—Yellow-poplar seeds must overwinter under natural conditions, or be stratified under controlled conditions, to overcome dormancy. Under controlled conditions, stratification in moist sand within a temperature range of 0° to 10° C (32° to 50° F) for periods of 70 to 90 days resulted in satisfactory germination. However, seedling yield increases with increasing time of stratification. Germination is epigeal.

Germinating yellow-poplar seedlings need a suitable seedbed and adequate moisture to survive and become established. Seed germination and seedling development is better on mineral soils or well-decomposed organic matter than on a thick, undecomposed litter layer.

Scarification and fires, which put seeds in contact with mineral soil, increases the number of seedlings established significantly *(10,33)*. Under normal conditions, however, the site disturbance caused by logging the mature stand is the only seedbed preparation needed to provide enough yellow-poplar seedlings for a new stand. In Indiana, 1 year after cutting, there were 9,900 yellow-poplar seedlings per hectare (4,000/acre) on a plot that was clearcut, and 12,000/ha (4,800/acre) on partially cut plots. In western North Carolina, more than 124,000 seedlings/ha (50,000/acre) followed both clearcuts and partial cuts that removed as little as one-third the basal area *(26)*. On occasional sites, deep accumulations of litter may require some seedbed treatment, particularly on the drier sites dominated by oaks or beech, and both disking and burning have proven effective. These treatments have also been recommended for sites with few seeds in the forest floor, especially if the site is covered with dense herbaceous growth.

Yellow-poplar seedlings reach maximum or near-maximum photosynthetic efficiency at relatively low light intensities, as low as 3 to 10 percent of full sunlight *(29,31)*. Growth was poor, however, under an overstory canopy where the amount of sunlight reaching the forest floor was limited to 1.33 percent; where herbaceous cover existed, it was only 0.13 percent. Sufficient sunlight can be admitted by various cutting practices. Harvest cuts ranging from removal of 30 percent of basal area to complete clearcuts have resulted in establishment and growth of large numbers of seedlings. Clearcutting, seed-tree cutting, and shelterwood cutting have all been used successfully to regenerate yellow-poplar *(26,28,38,45)*. However, when partial cuts such as shelterwood are used, height growth is severely limited by the overstory. Seedlings in clearcuts may be two to three times taller than seedlings under a shelterwood after the first 5 to 10 years.

The minimum size opening that can be used to regenerate yellow-poplar is fairly small *(10)*. Numbers of seedlings per hectare vary little in openings of 0.12 to 12.36 ha (0.05 to 5 acres). Opening size, however, does affect growth significantly. Both diameter and height are retarded in openings smaller than 1.24 to 2.47 ha (0.5 to 1 acre).

Season of logging, though not of critical importance, does have some effect on establishment and growth of yellow-poplar seedlings *(40)*. In West Virginia, Ohio, and Indiana, summer logging produced fewer seedlings than logging at other times of the year. Apparently, in summer-logged stands most of the seeds did not germinate until the following year, and these small seedlings were not as well able to compete with the rank vegetation that started the previous year. Nevertheless, cuttings in summer months usually have produced sufficient seedlings where a good seed source previously was present. If seed supply is expected to be scarce, logging in fall, winter, or early spring might be advisable.

After germination, several critical years follow. During this period sufficient soil moisture must be available, good drainage and protection against drying and frost heaving are necessary, and there must be no severe competition from nearby sprout growth. In a study in which various mulches were used to induce soil temperature variation, seedlings grew faster in warm soil than in cool soil. Soil temperatures as high as 36.1° C (97° F) had a beneficial effect on seedling growth. Yellow-poplar seedlings normally survive dormant-season flooding, but it was found that 1-year-old seedlings were usually killed by 4 days or more of flooding during the growing season *(23)*. This vulnerability during the growing season explains why yellow-poplar does not grow on flood plains of rivers that flood periodically for several days at a time. After the first growing season, vegetative competition may become the most important factor affecting survival and growth. Reducing competition by cutting, burning, disking, or by using herbicides may be needed to assure success.

On favorable sites the success of regeneration can usually be determined by the size and vigor of the seedlings at the end of the third year. Height growth during the first year ranges from a few centimeters to more than 0.3 m (1 ft) on the best sites. With full light, rapid height growth begins the second year, and at the end of 5 years trees may be 3 to 5.5 m (10 to 18 ft) tall. During its seedling and sapling stages, yellow-poplar is capable of making extremely rapid growth. An 11-year-old natural seedling 15.2 m (50 ft) tall has been recorded.

The behavior and duration of height growth of yellow-poplar vary by latitude. In a Pennsylvania study, seedlings had a 95-day height-growth period beginning late in April and ending about August 1. A sharp peak in height growth was reached about June 1. In a northwestern Connecticut study, yellow-poplar had a 110-day height-growth period beginning in late April and ending in mid-August. Ninety percent of this growth took place in a 60-day period from May 20 to July 20, and a sharp peak in height growth was noted in the middle of June. In a study conducted in the lower Piedmont of North Carolina, yellow-poplar had a 160-day height-growth period beginning in early April and ending about the middle of September. Growth was fairly constant, and there was no peak in growth rate during the growing season.

Vegetative Reproduction—Yellow-poplar sprouts arise chiefly from preexisting dormant buds situated near the base of dead or dying stems, or near the soil line on stumps. Sprouts may occur as high as 30 to 38 cm (12 to 15 in) on high stumps, but more than 80 percent arise at or below the soil line *(44)*. The percentage of stumps sprouting and the number of sprouts per stump decrease with increasing stump size. Stumps as large as 66 to 76 cm (26 to 30 in) sprouted 40 percent of the time, however, with an average of eight sprouts per stump. Yellow-poplar of the age and size harvested in second-growth stands sprouts prolifically.

Trees of sprout origin are more subject to butt rot than those of seedling origin *(42)*. Nevertheless, a high percentage of stumps that sprout produce at least one stem that is well anchored, vigorous, and of desirable quality for crop-tree development *(20)*. In this respect, position on stump is important to subsequent development. Sprouts arising from roots or from the stump below groundline usually lack a heartwood connection with the stump heartwood because the roots and below-ground portions of the stump do not normally contain heartwood. Sapwood tissues separating heartwood columns of stumps and sprouts may prevent heart rot fungi, which enters the stump heartwood, from spreading to the heartwood of the sprout.

The initial growth rate of yellow-poplar sprouts far exceeds that of young seedlings. In western North Carolina, the dominant sprout on each of 60 stumps on a good site grew an average of 1.4 m (4.7 ft) per year over the first 6 years *(2)*. At age 24, these sprouts averaged 24.4 m (80 ft) in height and 24 cm (9.6 in) d.b.h. In West Virginia, the dominant stem of each sprout clump grew at the rate of 0.9 m (2.9 ft) per year for 11 years on a medium-quality site for yellow-poplar *(44)*. The rapid, early growth rate begins to drop off markedly somewhere between 20 and 30 years. At this time, seedlings of similar age may catch up and exceed sprouts in rate of height growth.

A number of investigators have attempted to root yellow-poplar cuttings, but most early attempts were not successful. In a more recent study, cuttings were rooted successfully after they were dipped in dolebutyric acid and a mist of water was sprayed over the propagation bed *(6)*. It is not known, however, whether these rooted cuttings would have successfully survived outplanting. Yellow-poplar has been successfully rooted from stump sprouts of 7-year-old trees; soft-tissue cuttings placed in a mist bed began rooting in 4 weeks and successfully survived transplanting. A system of splitting seedlings longitudinally and then propagating the halves was also highly successful. However, splitting seedlings provides only one additional new plant from the ortet, while rooting stump sprouts provides several.

A technique for propagating yellow-poplar by making use of its epicormic branching ability has recently been described *(24)*. Partial girdling into the outer one or two annual rings results in a profusion of epicormic sprouts that can then be rooted in the same way as stump sprouts. This method has the advantage of preserving the selected ortet for repeated use. Experience with this method, however, reveals that not every girdled tree will sprout well. Young trees and trees with low vigor are better sprouters than old trees and rapidly growing trees.

Sapling and Pole Stages to Maturity

Growth and Yield—The mature yellow-poplar has a striking appearance. In forest stands its trunk is very straight, tall, and clear of lateral branches for a considerable height. It is among the tallest of all Eastern United States broadleaf trees. On the best sites, old-growth trees may be nearly 61 m (200 ft) high and 2.4 to 3.7 m (8 to 12 ft) d.b.h., but more often they are from 30.5 to 45.7 m (100 to 150 ft) at

Table 1—Height and d.b.h. of dominant yellow-poplar trees in unthinned stands, by site index *(1,3)*[1]

Age	Site index					
	25 m or 82 ft		30 m or 98 ft		35 m or 125 ft	
	Height	D.b.h.	Height	D.b.h.	Height	D.b.h.
yr	*m*	*cm*	*m*	*cm*	*m*	*cm*
20	13.4	17	15.8	21	18.6	25
30	18.9	25	22.6	30	26.5	36
40	22.6	30	27.1	37	31.4	43
50	25.0	34	29.9	41	35.1	48
60	26.8	37	32.3	44	37.5	52
70	28.3	39	33.3	46	39.6	55
80	29.3	40	35.1	49	41.1	57
90	30.2	41	36.3	50	42.1	59
100	30.8	42	36.9	51	43.3	60
yr	*ft*	*in*	*ft*	*in*	*ft*	*in*
20	44	6.7	52	8.2	61	9.8
30	62	9.9	74	12.0	87	14.2
40	74	12.0	89	14.5	103	17.0
50	82	13.4	98	16.2	115	19.0
60	88	14.4	106	17.4	123	20.4
70	93	15.2	111	18.3	130	21.6
80	96	15.8	115	19.1	135	22.4
90	99	16.3	119	19.7	138	23.1
100	101	16.7	121	20.2	142	23.7

[1] Based upon the average height and d.b.h. of the 62 largest trees per hectare (25/acre)

maturity, with a straight trunk 0.6 to 1.5 m (2 to 5 ft) in diameter. Age at natural death is usually about 200 to 250 years. However, some trees may live up to 300 years.

Height and d.b.h. expected of the 25 largest trees per acre in unthinned second-growth southern Appalachian stands are shown in table 1. These data represent an average dominant tree grown under fully stocked stand conditions. The largest trees would be 7.6 to 12.7 cm (3 to 5 in) larger than the average dominant at comparable ages. Table 2 shows selected empirical yields for natural stands *(3,27)*. Mean annual increment in total cubic volume ranges from 5.2 to 11.6 m^3/ha (75 to 165 ft^3/acre), depending on site, at culmination around 70 years of age.

Rooting Habit—Yellow-poplar has a rapidly growing and deeply penetrating juvenile taproot, as well as many strongly developed and wide-spreading lateral roots. It is considered to have a "flexible" rooting habit, even in the juvenile stage.

Reaction to Competition—Although classed as intolerant of shade, yellow-poplar can overcome much competition because it produces numerous seedlings and sprouts, and grows very rapidly. On land of site index 23 m (75 ft) and higher in the southern Appalachians, yellow-poplar has faster height growth than any of its associates except white pine up to 50 years of age *(29)*. If not overtopped, yellow-poplar takes and holds its place in the dominant crown canopy of the developing stand.

It is often a pioneer on abandoned old fields or clearcut land and may form essentially pure stands on very good sites. More often it regenerates as a mixed type with other species, and it commonly persists in old-growth stands as scattered individuals.

Yellow-poplar expresses dominance well and seldom, if ever, stagnates because of excessive stand density. It prunes very well in closed stands. Although it produces epicormic sprouts when the bole is exposed, this trait is less pronounced than in many

Table 2—Empirical yields for unthinned yellow-poplar stands in the southern Appalachians[1]

Basal area	Volume by age class in years[2]				
	20	30	40	50	60
m^2/ha			*m^3/ha*		
			Site index 25 m		
15	68	94	110	121	129
25	150	207	243	267	285
35	253	348	409	450	480
			Site index 30 m		
15	82	113	132	146	155
25	181	249	292	321	342
35	304	418	491	540	576
			Site index 35 m		
15	93	129	151	166	177
25	206	283	332	366	390
35	346	477	559	616	656
ft^2/acre			*ft^3/acre*		
			Site index 82 ft		
65	974	1,341	1,574	1,732	1,847
109	2,147	2,956	3,469	3,818	4,070
152	3,614	4,976	5,839	6,427	6,851
			Site index 98 ft		
65	1,170	1,611	1,890	2,080	2,218
109	2,579	3,551	4,166	4,586	4,889
152	4,341	5,976	7,012	7,718	8,228
			Site index 115 ft		
65	1,333	1,836	2,154	2,371	2,528
109	2,939	4,047	4,749	5,227	5,572
152	4,947	6,812	7,992	8,797	9,378

[1] All trees 13 cm (5 in) and larger in d.b.h.

[2] Volume includes wood and bark of the entire bole

other hardwood species. Because of these growth characteristics, yellow-poplar stands can develop and produce considerable quantities of large, high-quality products with no intermediate stand management.

In the seedling-sapling stage, dominant and codominant trees are little affected by thinning or cleaning *(21,39)*. Intermediate or overtopped trees of good vigor respond to release in both diameter and height growth *(46)*. Cultural treatment of seedling-sapling stands is seldom needed or justified, however, except to remove vines *(12)*.

By the time stands reach pole size at 20 to 30 years of age the peak rates of growth and mortality are past and the crown canopy is closed. Crown size on surviving trees is reduced and diameter growth is considerably slowed. Thinnings that salvage or prevent mortality, increase the growth of residual trees, shorten rotations, and increase the yield of high-value timber products are the essence of intermediate stand management. The net result of numerous thinning experiments is that individual yellow-poplar trees tend to use the space and accelerate diameter increment *(4,5,9,29)*. Response occurs across a wide range of sites and stand ages, even in stands as old as 80 years that have never been thinned previously. Total cubic-volume growth is greatest at the highest densities and would be maximized by very light, frequent thinnings that prevent or salvage mortality. On the other hand, board-foot volume growth is maximum at densities well below those that maximize cubic-foot volume growth. Board-foot growth is near maximum over a wide range of density. Thus, there is considerable leeway to manipulate stocking levels to achieve diameter growth and quality goals without sacrificing volume growth of the high-value products.

Damaging Agents—Yellow-poplar is unusually free from damage by pests compared with many other commercially important species. While more than 30 species of insects attack yellow-poplar, only 4 species are considered to have significant economic impact *(8)*. The tuliptree scale *(Toumeyella liriodendri)* causes loss of vigor by removing large quantities of phloem sap. Scale attacks often kill leaders of seedlings and saplings causing them to be overtopped by competitors. The yellow-poplar weevil *(Odontopus calceatus)* feeds on buds and foliage and may occur in outbreaks over large areas. The root-collar borer *(Euzophera ostricolorella)* attacks the phloem tissue at the base of the tree and provides entry points for rots and other pathogens. Attacks by the Columbian timber beetle *(Corthylus columbianus)* do not kill the tree but may degrade the wood. The defect consists of black-stained burrows and discolored wood called "calico poplar."

Fire scars, logging damage, animal and bird damage, top breakage, dying limbs, and decaying parent stumps all provide entry for decay-causing fungi *(16)*. Probably the most common type of decay associated with basal wounding and decaying stumps is a soft, spongy, white or gray rot caused by the fungus *Armillaria mellea*. A white heartwood rot caused by *Collybia velutipes* often is associated with top breakage and dying limbs. Species of the genus *Nectria* have been associated with stem cankers. Incidence of this disease and mortality from it was greatest on low-vigor trees.

A canker caused by *Fusarium solani* was isolated from large yellow-poplars in Ohio and was shown to cause characteristic cankers through pathogenicity studies. Some mortality results during periods of drought, but *F. solani* apparently is not a virulent pathogen and causes damage only when the host is weakened by unfavorable environmental factors.

Dieback and associated stem canker of yellow-poplar saplings were reported to have resulted in considerable mortality in some stands. A fungus of the genus *Myxosporium* was associated with dead bark of infected trees and was shown to cause canker formation after experimental inoculations. Identical dieback symptoms were reported for scattered areas throughout the South. Symptoms included chlorosis of leaves, sparse crown, dieback, trunk and branch cankers, and epicormic sprouting. Several fungal species were consistently isolated from cankered trees, but there was uncertainty about the causative agent. The severity and extent of infection are greater in upland sites than in bottom-land sites. All canker-forming diseases reported for yellow-poplar appear to be confined to, or most severe on, trees that are low in vigor because of drought, poor site, or competition.

A nursery root-rot disease caused by *Cylindrocladium scoparium* causes root and stem lesions. It is frequently lethal in nursery beds and causes low survival and poor growth when infected seedlings are outplanted. Extensive root damage and mortality in a 27-year-old yellow-poplar plantation have been reported.

Yellow-poplar logs, especially when cut in warmer seasons, are subject to rapid deterioration because of attacks of wood-staining fungi that feed largely on the starch and sugars in the green sapwood and penetrate deeply while the wood is moist. The most common rapid-staining species is *Ceratocystis pluriannulata*.

Yellow-poplar seedlings and saplings have thin bark and are extremely susceptible to fire damage.

Even a light ground fire is usually fatal to small stems up to 2.5 cm (1 in) in diameter. These stems resprout after fire, but repeated fires may eliminate yellow-poplar from a site. When the bark becomes thick enough to insulate the cambium (about 1.3 cm; 0.5 in), yellow-poplar becomes extremely fire resistant.

Sleet and glaze storms, which occur periodically within the range of yellow-poplar, may cause considerable damage. Stump sprouts are particularly susceptible to injury, slender trees may be broken off, and tops of dominant and codominant trees are often broken. Top damage is often the point of entry for fungi. Although yellow-poplar usually makes remarkable recovery after such storms, repeated damage can result in a growth reduction and loss of quality.

The leaves, twigs, and branches of yellow-poplar are tender and palatable to livestock and white-tailed deer, and young trees are often heavily browsed. Seedlings are grazed to the ground, small saplings are trimmed back, and even large saplings may be ridden down and severely damaged. In areas where animals are concentrated, young yellow-poplar is frequently eliminated. Rabbits also eat the bark and buds of seedlings and saplings and can be quite destructive at times.

When the sap is running in the spring, yellow-poplar is very susceptible to logging damage. If a falling tree strikes a standing poplar, there is often considerable bark loss up and down the bole of the standing tree. Even if the bark appears only lightly bruised, it may subsequently dry up and fall off in long strips.

Frost, especially in frost pockets, can affect the early growth and development of yellow-poplar. Following a late spring frost in a 20-year-old plantation, it was found that leaf mortality varied from 5 to 100 percent of the leaves on the individual trees. Leaf mortality was lowest on trees with a high foliar content of potassium. Frost may also cause bole damage in the form of shake, a separation of growth rings resulting in cull. A weather-induced defect called blister shake, related to frost shake, was described in 30-year-old yellow-poplar trees in West Virginia.

Vines can be extremely damaging to yellow-poplar. Japanese honeysuckle *(Lonicera japonica)*, kudzu *(Pueraria lobata)*, and climbing bittersweet *(Celastrus scandens)* have been known to have deleterious effects on yellow-poplar in isolated cases. However, the most widespread damage throughout the Appalachians results from wild grapevines *(Vitis* spp.) *(36,41)*, particularly on good sites that have been regenerated naturally by clearcutting. Many forest managers and researchers consider grape the most serious threat to production of high-quality yellow-poplar timber in the Appalachian region. Grapevines damage young trees by breaking limbs and tops, twisting and bending the main stem, and intercepting solar radiation. The result is reduced growth, malformation of stem and crown, and sometimes death of the trees. Grapevines also worsen winter storm damage in some areas by furnishing increased surface area for accumulation of ice and snow.

Special Uses

Yellow-poplar is an extremely versatile wood with a multitude of uses. Most important recent uses of the wood have been for lumber for unexposed furniture parts and core stock, rotary-cut veneer for use as crossbands in construction of furniture parts, in plywood for backs and interior parts, and as pulpwood. Considerable attention is being given to its use as structural framing material and for veneers in structural plywood as a substitute for increasingly scarce softwoods.

Yellow-poplar, with its shiny green leaves, distinctive flower, and statuesque appearance, is an excellent ornamental for park and garden where there is adequate space to accommodate its large size. It has distinctive value as a honey tree *(25)*. In one season a tree less than 20 years old reportedly yields 3.6 kg (8 lb) of nectar equal to 1.8 kg (4 lb) of honey. It has nominal value as a source of wildlife food in comparison to some other species, but its seeds are eaten by quails, purple finches, rabbits, gray squirrels, and white-footed mice. Because of its greater volume per acre, which is due to its greater density and height, yellow-poplar on very good sites may produce more dry-weight yield per acre than species such as oak with much denser wood. It may have potential as a producer of wood fiber for energy and other uses.

Genetics

Population Differences

The significant variation in many traits among individual trees, among stands, and between geographic sources of yellow-poplar *(15,29,34)* is of interest to forest managers and users of wood products.

Varying degrees of genetic control have been demonstrated for wood and tree properties such as specific gravity and fiber length; straightness; branch angle; natural pruning ability; leaf, fruit, and seed characteristics; disease resistance; growth of seedlings; and length of growing season. For other important traits, such as the tendency to produce epicormic sprouts, evidence exists that the trait is strongly inherited although this has not yet been demonstrated conclusively.

A growth chamber study revealed that seedlings of northern and southern origin responded very differently to day-length treatments *(43)*. A day length of 18 hours inhibited the northern source but not the southern. The most consistent difference among geographic seed sources has appeared in dormancy relationships. In general, the more northern sources start growth later and cease earlier than the more southern sources. Few studies are old enough to permit good comparisons of volume differences for different seed sources, but significant differences in early height growth have been reported.

While most geographic differences are associated with latitude of source, there are good indications that environmental differences associated with altitude are also important. In North Carolina, a clinal pattern of variation existed from coast to mountain for a number of seed and leaf characteristics *(19)*.

Races

At least one distinct ecotype of yellow-poplar has been confirmed. First evidence came from a plantation near Charleston, SC, where trees from a Coastal Plain source in eastern North Carolina were twice as tall 3 years after outplanting as those from a mountain source in western North Carolina *(29)*. Later, a source from the Coastal Plain of North Carolina performed poorly in comparison to upland sources when planted at a Piedmont location but was far superior to upland sources when planted on organic soils of the Coastal Plain where pH values seldom exceed 4.0 *(19)*. Yellow-poplar of the coastal source has a distinctive leaf pattern and color—rounded lobes and copperish-red leaves. It is apparently adapted to the highly acidic, water-saturated organic soils of the Coastal Plain and is able to withstand periodic inundation without harm *(32)*. Sources with the distinctive leaf characteristics have been found as far south as Florida.

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Lithocarpus densiflorus (Hook. & Arn.) Rehd. **Tanoak**

Fagaceae **Beech family**

John C. Tappeiner, II, Philip M. McDonald, Douglass F. Roy

Tanoak *(Lithocarpus densiflorus)*, also called tanbark-oak, is an evergreen hardwood that, with other species in the genus, is considered a link between the chestnut, *Castanea*, and the oak, *Quercus* (*19*). Tanoak has flowers like the chestnut and acorns like the oak. This medium-sized tree grows best on the humid moist slopes of the seaward coastal ranges. It usually occurs in a complex mixture with conifers and other hardwoods, but often forms pure even-aged stands. The wood is hard, strong, and fine-grained. Tanoak is designated a commercial species in California. Current major uses are for fuel and pulp. The acorns are a valuable food source for many kinds of wildlife.

Habitat

Native Range

A disjunct stand slightly north of the Umpqua River in southwestern Oregon has been reported as the northernmost limit of tanoak's natural range (fig. 1). The general northern limit of tanoak in the Coast Ranges, however, is farther south in the Coquille River drainage. Its eastern limit in Oregon extends from west of Roseburg to Grants Pass, and then southwesterly into the Applegate River drainage. Tanoak's range stretches southward through the Coast Ranges in California to the Santa Ynez Mountains north and east of Santa Barbara, CA. The range also extends northeastward from the Humboldt Bay region to the lower slopes of Mount Shasta, then intermittently southward along the western slopes of the Sierra Nevada as far as Mariposa County (*7*). In the Sierra Nevada, tanoak is most common between the Feather and American Rivers.

Climate

Tanoak grows in a climate broadly classified as humid. Annual precipitation, however, is seasonal and varies from 1020 to 2540 mm (40 to 100 in). Some precipitation is snow. Summer and early fall are dry and the winter rainy. From June through September rainfall totals less than 25 mm (1 in) a month. In fact, precipitation during these months amounts to only 5 percent of the year's total. Most of the precipitation—about 70 percent—falls between November and February.

Average mean daily temperatures range from 2° to 6° C (36° to 42° F) during January and 16° to 23° C (60° to 74° F) in July. The season free of killing frosts begins between March 8 and April 30 and ends between October 20 and November 20, varying in length between 160 and 249 days. Over a 30-year period the maximum temperature recorded at 183 m (600 ft) elevation in the center of tanoak's area of maximum development was 45° C (113° F).

Soils and Topography

Tanoak grows well on a variety of soils developed from igneous, metamorphic, or sedimentary rocks, or sedimentary rock alluvium. It grows best on soils that are deep, well-drained, and loamy, sandy, or gravelly. Tanoak also grows on soils derived from serpentine, which are intermediate between the moist and dry extremes, but is limited to a shrubby form. It is seldom found on heavy clayey soils.

High-site soils for redwood (*Sequoia sempervirens*) or Douglas-fir (*Pseudotsuga menziesii*), such as the Hugo, Sheetiron, Josephine, Empire, Larabee, Sites, and Melbourne (*12*) series, are also well suited for the growth of tanoak (*28*). These soils have been derived from either consolidated or soft sedimentary rocks. They are light grayish brown or light reddish brown to brown in color and are moderately to strongly acidic. Soil textures grade through gravelly loam, sand loam, fine sandy loam, loam, silt loam, to clay loam. Soil orders are mostly Inceptisols and Alfisols.

Besides growing well on deep soils, tanoak also thrives on stony and shallow soils that are less suitable for conifers. Yet tanoak requires more moisture than many other hardwoods. It will grow well on the shallow and stony soils of north slopes, for example, but will be supplanted by Pacific madrone (*Arbutus menziesii*), Oregon white oak (*Quercus garryana*), or California black oak (*Q. kelloggii*) on the warmer, drier south slopes.

Throughout the Coast Ranges from the northern limit of tanoak's distribution (lat. 43° 42′ N.) to the Santa Lucia Mountains (lat. 35° 40′ N.) tanoak grows from sea level to elevations of 1220 or 1525 m (4,000 or 5,000 ft). The terrain is rough, steep, and extremely dissected by both major streams and smaller

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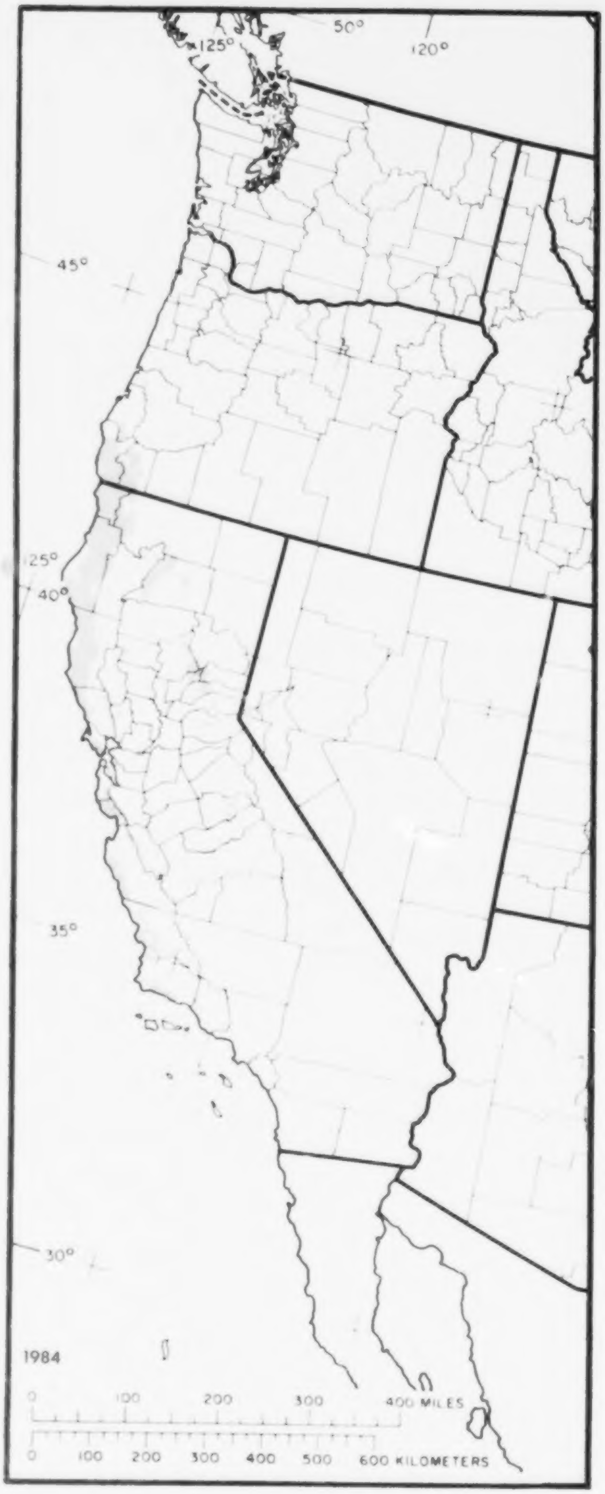

Figure 1—*The native range of tanoak.*

drainages. In the Santa Ynez Mountains, at the southern limit of its range (lat. 34° 34′ N.), tanoak grows at 730 to 1435 m (2,400 to 4,700 ft). In the northern Sierra Nevada, it grows between elevations of 580 and 1220 m (1,900 and 4,000 ft) and in the central Sierra Nevada between 915 and 1525 m (3,000 and 5,000 ft). At its southern limit in the Sierra Nevada, tanoak is found between 1525 to 1980 m (5,000 and 6,500 ft) near Signal Peak (lat. 37° 32′ N.) in the Sierra National Forest *(24)*.

Tanoak is most abundant and, in general, attains its largest sizes in Humboldt and Mendocino Counties, CA, between elevations of 150 to 915 m (500 to 3,000 ft) on northerly and easterly slopes and toward the summits of the seaward exposures of the Coast Ranges. In the southern Coast Ranges, tanoak is common in the Santa Cruz and Santa Lucia Mountains, particularly on the westerly slopes. And in the central Sierra Nevada, where the climate is less humid, it grows in valleys, coves, ravines, along streams, and on north slopes.

Associated Forest Cover

Tanoak grows within the life zones classified as the Canadian and Transition. It is the most abundant hardwood species in timber stands of the Coast Ranges of California *(6)* and southwestern Oregon. Tanoak is a common component in the following forest cover types *(4)*: Redwood (Society of American Foresters Type 232), Pacific Ponderosa Pine (Type 245), Pacific Ponderosa Pine—Douglas-Fir (Type 244), Sierra Nevada Mixed Conifer (Type 243), and California Coast Live Oak (Type 255). It is a particularly important component of Pacific Douglas-Fir (Type 229) and Douglas-Fir—Tanoak—Pacific Madrone (Type 234).

The principal body of tanoak is a broad band along the inland side of the redwood belt. Here tanoak sometimes forms almost pure stands *(6)*. More often it is an understory tree with Douglas-fir or is a component of hardwood stands or mixed hardwood-conifer forests (fig. 2). The most common hardwood associated with tanoak is Pacific madrone. Other frequent hardwood associates include giant chinkapin *(Castanopsis chrysophylla)*, canyon live oak *(Quercus chrysolepis)*, California black oak *(Q. kelloggii)*, and California-laurel *(Umbellularia californica)*. Tanoak is found most often with Douglas-fir and redwood. Other common conifer associates are California white fir *(Abies concolor* var. *lowiana)*, Sitka spruce *(Picea sitchensis)*, sugar pine *(Pinus lambertiana)*, ponderosa pine *(P. ponderosa* var. *ponderosa)*, California torreya (nutmeg) *(Torreya californica)*, and western hemlock *(Tsuga heterophylla)*.

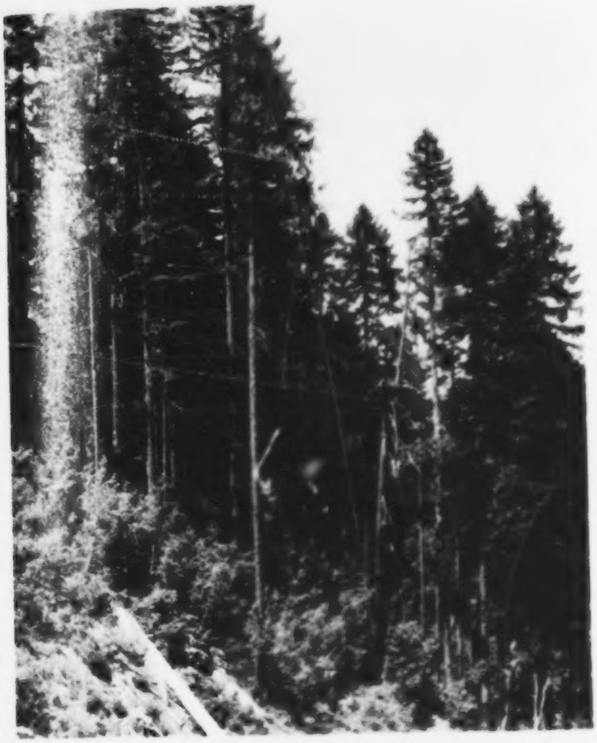

Figure 2—*Tanoak growing as understory trees in a stand of Douglas-fir* (*SAF 229*).

A large variety of shrubs, forbs, grasses, sedges, and ferns are also associated with tanoak. Generally these plants are not abundant on forested land, but, with tanoak sprouts, often become aggressive on burned or cutover areas. Among the most common shrubs are blueblossom (*Ceanothus thyrsiflorus*), California hazel (*Corylus cornuta* var. *californica*), salal (*Gaultheria shallon*), Pacific bayberry (*Myrica californica*), Pacific rhododendron (*Rhododendron macrophyllum*), flowering currant (*Ribes sanguineum*), thimbleberry (*Rubus parviflorus*), western poison-oak (*Toxicodendron diversilobum*), and California huckleberry (*Vaccinium ovatum*).

Also smaller plants producing woody growth above ground are prince's-pine (*Chimaphila umbellata* var. *occidentalis*) and Oregon grape (*Berberis nervosa*). Many forbs and grasses are plentiful in the tanoak range. Among the most important forbs are bull thistle (*Cirsium vulgare*), New Zealand fireweed (*Erechtites arguta*), Australian fireweed (*E. minima*), and western whipplea (*Whipplea modesta*). Common grass species include California brome (*Bromus carinatus*), soft chess (*B. mollis*), California fescue (*Festuca californica*), and California sweetgrass (*Hierochloe occidentalis*). Western swordfern (*Polystichum munitum*) and western bracken (*Pteridium aquilinum* var. *pubescens*) sometimes grow abundantly with tanoak. Sedges (*Carex* spp.) also are represented in some places.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Staminate catkins are elongate and erect, 5 to 10 cm (2 to 4 in) long. Blossoms may appear in the spring, summer, or autumn. However, most tanoaks bloom in June, July, or August. Trees at lower elevations and near the coast bloom earlier than trees at higher elevations and farther inland. The plant is monoecious.

Almost all the flowers, both male and female, are borne on new shoots (*22*), where they grow from the axils of the new leaves. Flowers also occasionally develop from buds found at the base of leaves of the previous year's growth.

Female flowers are borne at the base of erect male catkins. The profusion of yellowish blossoms that sometimes conceal the foliage suggested the tree's specific scientific name. The calyx is pale green; the stamen filament is white; and the anther yellow.

The seeds, which are similar to oak acorns, ripen in the second autumn. Seeds are usually borne singly, in twos, or in threes (*25*), but sometimes more are clustered together.

Seed Production and Dissemination—Tanoak is a heavy seeder (*3*). In general, viable seeds are borne in abundance after the 30th to 40th year (*8*), although 5-year-old sprouts also have produced fairly heavy crops. A long dry period at pollination time helps the setting of acorns. Trees are heavily laden almost every alternate year, and complete seed crop failures are rare. "Jayhawking"—peeling the bark from standing trees—has shown that girdling produces excessively large acorn crops before the trees die. Scanty crops generally are caused by frosts or by a dry year.

Mature trees produce the most acorns. One estimate places annual acorn production of a veteran tanoak 76 cm (30 in) in d.b.h. at about 454 kg (1,000 lb). Because about 110 acorns weigh 0.45 kg (1 lb), this production is more than 110,000 acorns. Other estimates showed that trees between 46 and 61 cm (18 and 24 in) d.b.h. produced 3,900 to 4,600 acorns.

Insects destroy a significant number of acorns. One study found insect larvae infesting 51 percent of the acorns. The insects identified were the filbert weevil

(*Curculio uniformis*) and the filbertworm (*Melissopus latiferreanus*). Other insect larvae that have been found in tanoak acorns are from the families *Gelechiidae* and *Pyralidae* (*5*).

Many immature acorns have been seen on the ground as early as August 25, but these were probably knocked down by heavy rains. Mature tanoak acorns drop between September 20 and November 15. The first acorns to fall are usually insect infested, whereas those falling later are usually sound. Indians in California placed a taboo on collecting acorns for food until their medicine women held a ceremonial festival that celebrated the falling of sound acorns.

Because the acorns are large—2.5 to 5.1 cm (1.0 to 2.0 in) long and 15 to 18 mm (0.6 to 0.7 in) in diameter—and heavy, most of them fall straight to the ground and are found under the tree crowns. Only a few bounce outward when dropping onto lower branches or roll for short distances on steep slopes. In one small study, acorns were counted under trees 46 to 61 cm (18 to 24 in) in diameter at rates of 194,000 to 226,000/ha (78,400 to 91,500/acre) (*24*).

Seedling Development—With suitable conditions, tanoak reproduces well from seed. Acorns germinate in a wide range of environments from old-growth stands to recent clearcuts (*31*). However, survival of unprotected seed is low in clearcuts due to heavy predation. The dense shade of virgin forests, and the thick litter found under tanoaks, madrones, or other hardwoods, do not hinder germination. Seedlings are common in these conditions. Tanoak germination is hypogeous.

A limited number of tests show that germination rates vary from 19 to 80 percent (*25*). When acorns were planted with pointed end up, germination was significantly greater (*13*).

Almost all natural seedlings emerge in the spring; some germination may occur in the fall, but only if the weather is mild and moist. To preserve their viability, tanoak acorns must either be planted immediately in the nursery in light soil, or be stratified until spring at temperatures just above freezing. Seedlings appear about 3 weeks after planting.

Natural tanoak seedlings have been counted under parent trees left after the Douglas-fir overstory had been cut. Although 1 year's acorn crop produced 395 to 940 seedlings per hectare (160 to 380 seedlings/acre) under trees 51 to 66 cm (20 to 26 in) d.b.h., the efficiency of sound acorns in producing seedlings was only 0.64 percent. Only one seedling grew from 156 sound acorns.

Many natural seedlings are found in the understory of conifer stands, which appears to be an ideal environment for reproduction (*29*). In southwestern Oregon, seedling survival after 4 years ranged from 44 to 49 percent in conifer stands whose ages ranged from 50 to 100+ years (*31*). In the northern Sierra Nevada, from 17 to 347 new seedlings per acre were present annually during an 11-year period (*13*). The annual appearance of new seedlings along with modest rates of mortality resulted in relatively stable populations of 570 to 3000/ha (233 to 1,215/acre) during these 11 years. However, attempts to establish a plantation of tanoak by artificial seeding on an exposed site, which had been prepared by removing vegetation and exposing mineral soil, were unsuccessful (*13*).

Biotic factors contribute to low seed crop efficiency. Although the acorns have hard seedcoats (the generic name, *Lithocarpus*, from the Greek "lithos" meaning rock, and "karpos" meaning fruit, alludes to the hard acorn—at least 38 species of animals eat them (*2*). Principal consumers include 4 bird species, 11 rodent species, deer, bears, and raccoons. Goats, hogs, and cattle also prevent seedling reproduction by devouring acorns and browsing tender seedlings.

Heights of first-year, natural tanoak seedlings, measured from cotyledons to growing tip, in one study varied from 5 to 21 cm (1.9 to 8.3 in) and averaged 13 cm (5.2 in), greater than first-year heights of natural conifers on the same site (*24*). After the first year, the seedling growth rate is moderate, less than 5.0 cm (2 in) per year.

Tanoak seedlings begin to produce burls below ground at 1 to 2 years of age. Burls develop more quickly on good sites and, in one study, averaged 25 mm (1.0 in) in diameter in 10 to 12 years (*29*). After 6 to 12 years, the original stem dies (even without browsing or other damage) and a new top is produced that tends to be more vigorous than the original one. Tanoak seedlings thus become seedling-sprouts. Top replacement is common, and seedling-sprouts may support several live stems (*29*). The tallest stem ranged from 25 to 150 cm (10 to 60 in) on 20-year-old seedling-sprouts in southwestern Oregon interior sites. More rapid development is likely in the coast range and northern Sierra Nevada forests. Tanoak seedling-sprout ages can be estimated by counting xylem rings in the stem below the burl, but there is no reliable relation between top age and/or size and total seedling-sprout age (*29*). The growth potential of seedling-sprouts is low. Forty- to fifty-year-old tanoak seedling-sprouts, for example, had burls that were only 5.0 to 7.5 cm (2 to 3 in) in diameter. Three years after removal of the overstory by cutting and burning, they produced clumps of 4 to 6 stems that averaged only 51 cm (20 in) tall.

Records on the seasonal growth of tanoak are scanty. Some observations have been recorded in the vicinity of Salyer, CA. Here, in the Trinity River valley and on the low mountain slopes up to 610 m (2,000 ft) elevation, tanoak vegetative buds open in mid-April. From 610 to 1065 m (2,000 to 3,500 ft), buds burst in mid-May, and from 1065 to 1340 m (3,500 to 4,400 ft), foliage growth begins in late May. At the elevational limit near Salyer, which is about 1370 m (4,500 ft), buds open in early June. Leaves persist for 3 to 4 years *(24)*.

The growing season lasts 4 to 5 months in the mountains and somewhat longer at lower elevations and nearer the coast.

Vegetative Reproduction—Tanoak reproduces prolifically by vigorous sprouts that appear at practically any time under a wide variety of conditions *(3)*. Sprouts may start to grow after a relatively minor basal injury, after bark has been stripped from the trees for tannin extraction, or when the aerial parts of the tree are destroyed by fire or logging *(22)*. Even healthy trees sometimes sprout.

Sprouts develop from conical woody buds that lie under the bark at the base of the tree. Most of these buds are found on burls below the groundline. Because the number of buds varies from few to thousands, the number of sprouts also varies. As many as 1,400 have been counted on one large stump. The only mechanical damage that prevents sprouting is stripping the bark below the ground level to expose the buds.

Sprouts from burls grow rapidly in a wide range of environments. In clearcuts, they have reached 1.7 m (5.6 ft) the first year and 4.1 m (13.6 ft) after 5 years. The microclimate within sprout clumps is quite different from the microclimate immediately adjoining them *(21)*. Sprout growth is reduced somewhat by a conifer overstory *(13)*. The size of parent trees between 3 and 43 cm (1.3 and 16.8 in) in d.b.h. determined the height and diameter growth of sprout clumps, and the number of sprouts in a clump. The larger parent trees produced greater sprout development [illegible]. Sprouts are reduced drastically in numbers early in their life and growth is concentrated on the dominant stems. In the first 15 or 20 years, sprouts grow an average of about 0.6 m (2 ft) in height a year. Often, a circle of four to eight slender 30-year-old poles grows around the stump of a parent tree. These poles may average 30 to 38 cm (12 to 15 in) in d.b.h. [illegible]. Thinning all but 2 to 4 sprouts per clump of 3- to [illegible]-year-old sprout clumps did not increase height or diameter growth of the remaining sprouts, largely

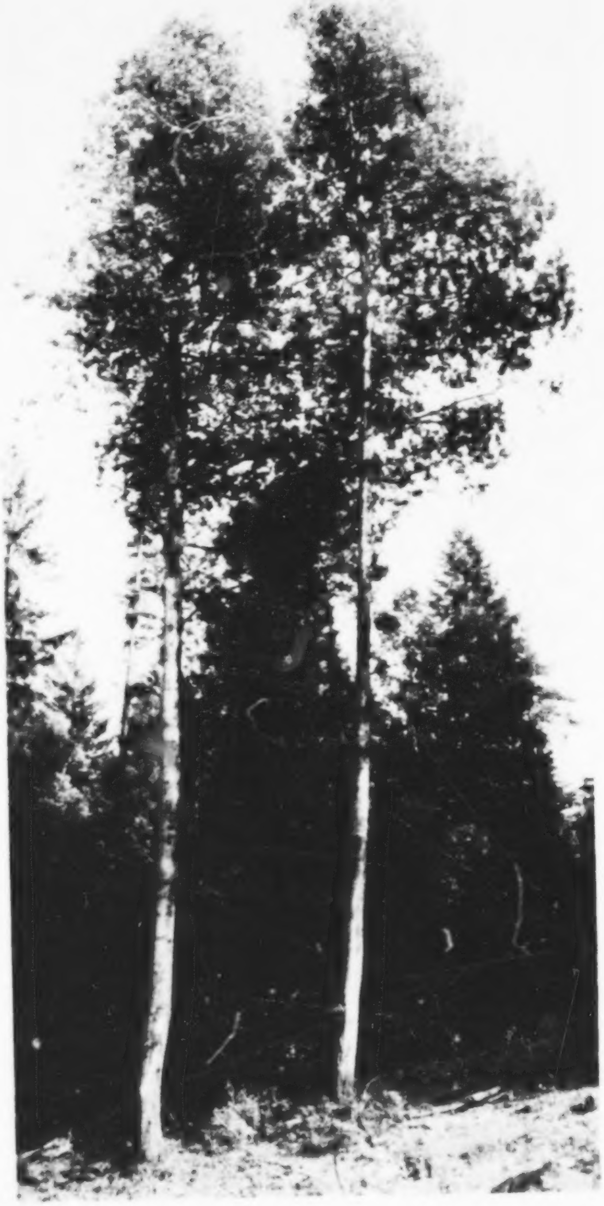

Figure 3—*Mature tanoaks of medium size. The tree on the left is 51 cm (20 in) and the one on the right is 46 cm (18 in) in d.b.h.; both are 22.9 m (75 ft) tall.*

because rapidly growing new sprouts quickly replaced those that had been cut *(14)*.

Leaf area, total above-ground biomass, height, clump width and area, and number of stems 1 to 6 years after cutting were statistically correlated with parent tree diameter at 1.4 m (4.5 ft) before cutting or burning *(9)*. Thus, sprout clump size and total stand cover can be predicted from stand stocking tables before harvesting or burning either conifer stands with a tanoak understory or pure tanoak stands *(30)*.

Although not growing as fast as sprouts of some associated hardwoods, such as bigleaf maple and madrone, tanoak sprouts are significant competitors because they are usually abundant, especially in conifer stands. Tanoak sprouts often quickly dominate the vegetational cover after logging or fire. Although this ability helps reduce soil erosion, tanoak sprouts often provide severe competition to conifer reproduction and may suppress it. The thick, stiff, flat, leathery leaves often cover young conifer seedlings or cover the ground so thoroughly that conifer seedlings cannot emerge above them *(20)*.

Propagation of tanoak by grafts or cuttings has not been reported.

Tanoak sprouts can be controlled by herbicides applied to frills on the stems, to stumps of freshly cut stems, or to foliage of young sprout clumps *(32)*.

Sapling and Pole Stages to Maturity

Growth and Yield—The form of tanoak varies greatly. In closed stands, particularly in dense coniferous forests, tanoaks develop one central axis, narrow crowns, ascending branches, and long trunks that are clear for 9.1 to 24.4 m (30 to 80 ft). In this form, tanoak is one of the most stately broadleaved trees in the West. In open stands, however, especially in association with Pacific madrone and California black oak, tanoaks are free branching, the crowns are broad, the limbs horizontal and large, and the trunks short and thick. The main trunk divides into several large branches and forms a rounded crown.

Tanoak is usually classed as medium in size *(15)*. Mature trees (fig. 3) are generally 15.2 to 27.4 m (50 to 90 ft) tall but frequently grow to 45.7 m (150 ft) *(26)*. The tallest tree reported was 63.4 m (208 ft) high and 137 cm (54 in) in d.b.h. It was found on the North Fork of the Little Sur River, Monterey County, CA.

Mature trees vary from 15 to 122 cm (6 to 48 in) in d.b.h. The largest diameter of record is 277 cm (109 in), measured on a tanoak near Kneeland, Humboldt County, CA. This tree was 30.5 m (100 ft) tall and the crown had a spread of 23.2 m (76 ft) *(1)*. Tanoaks with the largest diameters generally grow in open stands where tree heights are lower. Age-height-diameter relationships in Sonoma County, CA, were as follows *(24)*:

Age	Height		D.b.h.	
yr	*m*	*ft*	*cm*	*in*
20 to 40	9.1 to 15.2	30 to 50	10 to 23	4 to [illegible]
40 to 100	12.2 to 24.4	40 to 80	25 to 30	10 to [illegible]
70 to 125	24.4 to 30.5	80 to 100	33 to 46	13 to [illegible]
100 to 159	27.4 to 36.6	90 to 120	48 to 61	19 to [illegible]
125 to 180	35.1 to 42.7	115 to 140	64 to 91	25 to [illegible]
150 to 210	30.5 to 36.6	100 to 120	94 to 117	37 to [illegible]
170 to 250	30.5 to 36.6	100 to 120	119 to 152	47 to [illegible]

The growth of tanoak has been called slow, moderate, and fairly rapid. Knowledge about growth rate is limited, for only a few trees have been measured. Seven trees near Sherwood, Mendocino County, CA, which varied from 36 to 69 cm (14 to 27 in) in diameter at 0.61 m (2 ft) above the ground, had from 4 to 8 rings per centimeter (10 to 20/in). At another location, trees 48 years old averaged 25 cm (10 in) in d.b.h. and 10.7 m (35 ft) tall. Trees 36 to 46 cm (14 to 18 in) in d.b.h. were from 80 to 128 years old, and trees 51 to 152 cm (20 to 60 in) were from 150 to 250 years old.

It is difficult to ascertain the age of tanoak. As noted earlier, seedling sprouts in the understory were 50 to 60 years of age and less than 2 m (6 ft) tall. A tanoak taller than 20 m (60+ ft) had five stems ranging in size from 10 to 35 cm (4 to 12 in) d.b.h. and in age from 29 to 94 years *(29)*. It also had four burls below ground 35 to 90 cm (1.5 to 2.5 ft) d.b.h. in diameter, with scars of large stems 50 cm (1.5+ ft) which had died, broken off, and decayed. This tree was likely older than the 240-year-old conifers in the overstory. When the overstory is removed, sprouting tanoak forms an even-aged stand above ground, regardless of actual age.

Growth of tanoak stands 50 to 60 years old above ground thinned to six different basal-area densities (19 to 32 m^2/ha; 85 to 141 ft^2/acre) grew about 6 m^3/ha/yr (85 ft^3/acre/yr) for 8 years after thinning *(16)*.

Rooting Habit—Tanoaks develop deep taproots *(22)* and also develop intricate systems of lateral roots which may approach the soil surface and grow downhill, eventually emerging from the soil where they form burls that produce sprouts.

The sapwood of tanoak is extremely thick, reaching a high of 66 percent even on large trees. This condition helps trees to live after the bark has been stripped for tannin production or after trees have been girdled for eradication. Some girdled trees have lived as long as 30 years.

Reaction to Competition—Tanoak generally is classed as tolerant of shade *(22)*. It is aggressive and well fitted by its reproductive habits, vigor, and shade endurance to compete for possession of the ground *(31)*. Although tanoak can endure considerable shade throughout life, it grows best with top light. In conifer stands where it has an equal opportunity to grow, it can compete with redwood and Douglas-fir *(23)*. In dense stands, natural pruning produces long clear boles.

Tanoak can reproduce from both seed and sprouts and thus maintain itself in a wide range of forest types and successional stages. Under dense conifer stands it is often abundant (610 to 5300 stems/per hectare; 240 to 2,100/acre) *(29)*, and continuous input of new seedlings can maintain or increase stocking *(13)*. After the overstory is logged or burned, even small tanoaks can respond, and tanoaks of all sizes may dominate disturbed areas. Because of its ability to respond to disturbance and to reproduce and grow in the shade, it is considered to be a climax species in Douglas-fir, redwood, and mixed-conifer forests.

Damaging Agents—Fire is the principal enemy of individual tanoak trees *(3)*. Ground fires, as well as crown fires, are sometimes fatal. More often, however, fires leave long vertical wounds reaching from 1.2 to 3.0 m (4 to 10 ft) up the trunks. Although the bark of mature trees is at least 3 to 8 cm (1 to 3 in), and occasionally 10 or 13 cm (4 or 5 in) thick, some trees are burned badly.

Fire injuries to small trees often heal over, but fungi usually enter the wounds on older trees. The exposed wood on these larger trees rots and the wounds do not heal. If decayed wood catches fire it burns readily and the original wound is enlarged. Sometimes one-third to one-half the diameter of the tree is destroyed as a result of repeated fires and decay.

Until injured by fire, tanoak is relatively free from insect attacks and fungal diseases and is windfirm *(3)*. Injury to the trunk, however, allows fungi to enter. Wind and heavy snows eventually fell many trees originally injured by fire and subsequently weakened by decay.

Fire and fungi cause tanoak to be fairly defective. One study based upon cubic volume in 90 trees showed that the amounts of saw log cull were 39 percent in cull trees, 8 percent in noncull trees, and 18 percent in all trees.

Fungi found in living trees are the beefsteak fungus (*Fistulina hepatica*), which causes a brown cubical rot; the weeping conk (*Inonotus dryadeus*), a white root rot; and a necrophyte (*Schizophyllum commune*), which causes a sap rot on injured areas of standing trees. Tanoak is susceptible to the shoestring root disease (*Armillaria mellea*). The fungus *Ceuthocarpum conflictum* causes a commonly seen leafspot on tanoak *(10)*.

Several insects have been found feeding on tanoak but, generally, the damage is not economically significant. Two of these are armored scales identified as the greedy scale (*Hemiberlesia rapax*) and the oak scale (*Quernaspis quercus*). The greedy scale chiefly infests the bark but also feeds on leaves. The oak scale feeds on the undersides of leaves. Another insect, the crown whitefly (*Aleuroplatus coronatus*), resembles soft unarmored scales and feeds on the undersides of leaves, sometimes causing the leaves to fall prematurely. Ehrhorn's oak scale (*Mycetococcus ehrhorni*) is found on stems and the white sage mealybug (*Pseudococcus crawi*) on stems and leaves *(5)*.

In 1957, the California oakworm (*Phryganidia californica*) completely destroyed that year's foliage of tanoaks growing on Hennessey Ridge, near Salyer, Trinity County, CA. This damage was localized and was not observed at other places nearby. Usually, the California oakworm causes little damage but irregularly becomes epidemic over large areas.

Other insects work under the bark. Adults of the Pacific oak twig girdler, *Agrilus angelicus*, feed on foliage, but its larvae mine spiral galleries that girdle twigs, small limbs and trunks, or sprouts. Adults of a false powderpost beetle (*Melalgus confertus*) prune twigs by boring at the fork of small branches *(5)*.

Decline of tanoak sprout vigor was observed in mixed conifer-hardwood forests in the central Sierra Nevada *(18)*. Affected clumps were wider and denser, but only one-fifth as tall as unaffected clumps. Reason for the decline is not known.

Tanoak is avoided by livestock if better feed is available. Mule deer rarely browse it. The current year's growth of tanoak leaves and twigs is protected by abundant stellate trichomes, which are unpleasant to inhale.

Special Uses

The Indians in California's North Coast Range obtained one of their principal foods from tanoak. In fact, the main fare of many Indian communities was salmon and tanoak acorns. The large acorns were ground, leached, and then prepared as a soup, cooked mush, or a kind of bread. After being leached, the acorns are said to have an agreeable acid taste. They also contain a comparatively large amount of oil. On this account, tanoak acorns were preferred by local Indians over all other kinds. Ground tanoak acorns have also been fed to chickens.

Tannin from tanoak bark has properties intermediate between chestnut tannin and the usual oak tannin of commerce. The extract from tanoak bark, however, furnishes the best tannage known for the production of heavy leathers. For example, it gives excellent plumping when used to tan sole or saddle leather. The superiority of tanoak bark extract is attributed to the presence of certain other acids, such as gallic and acetic, with the tannic acid. Tanoak tannin has also been used medicinally as an astringent *(24)*.

One successful attempt to graft European chestnut *(Castanea sativa)* scions to tanoak stumps has been reported from southern Mendocino County.

Genetics

Races

A shrubby variety of tanoak *(L. densiflora* var. *echinoides)* grows near Mount Shasta, on the west slope of the northern Sierra Nevada, in the central Trinity Alps, in the Salmon and Klamath Mountains, and northward through the Siskiyou Mountains into southern Oregon *(28)*.

The shrub variety occupies a narrow elevational band just above that inhabited by the tree form. This variety is found on a wide range of soils including ultrabasics, but generally occurs only on moist sites *(27)*. On deep, productive soils, especially in the Sierra Nevada, it forms a dense cover of large clumps that often become flattened by snow. Stems from such clumps may straggle downslope for 5 m (16 ft) or more. After cutting or burning, upright sprout clumps are formed that closely resemble those of root crown sprouts from tanoak trees in clearcuttings *(17)*.

Small woody plants with slender, deeply toothed leaves were discovered in 1962 on the Challenge Experimental Forest, Yuba County, CA. These plants are believed to be a sublethal recessive mutation of tanoak and have been named *Lithocarpus densiflora* f. *attenuato-dentatus (33)*.

Hybrids

No hybrids of tanoak are known. Although *Lithocarpus* comprises between 100 and 200 species, all but tanoak are native to southeastern Asia and Indomalaysia *(11)*.

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Maclura pomifera (Raf.) Schneid. **Osage-Orange**

Moraceae Mulberry family

J. D. Burton

Osage-orange (*Maclura pomifera*) produces no sawtimber, pulpwood, or utility poles, but it has been planted in greater numbers than almost any other tree species in North America. Known also as hedge, hedge-apple, bodark, bois-d'arc, bowwood, and naranjo chino, it made agricultural settlement of the prairies possible (though not profitable), led directly to the invention of barbed wire, and then provided most of the posts for the wire that fenced the West. The heartwood, bark, and roots contain many extractives of actual and potential value in food processing, pesticide manufacturing, and dyemaking. Osage-orange is used in landscape design, being picturesque rather than beautiful, and possessing strong form, texture, and character.

Habitat

Native Range

The natural range of Osage-orange (fig. 1) is in the Red River drainage of Oklahoma, Texas, and Arkansas; and in the Blackland Prairies, Post Oak Savannas, and Chisos Mountains of Texas *(28)*. According to some authors the original range included most of eastern Oklahoma *(34)*, portions of Missouri *(49,54)*, and perhaps northwestern Louisiana *(28,49)*.

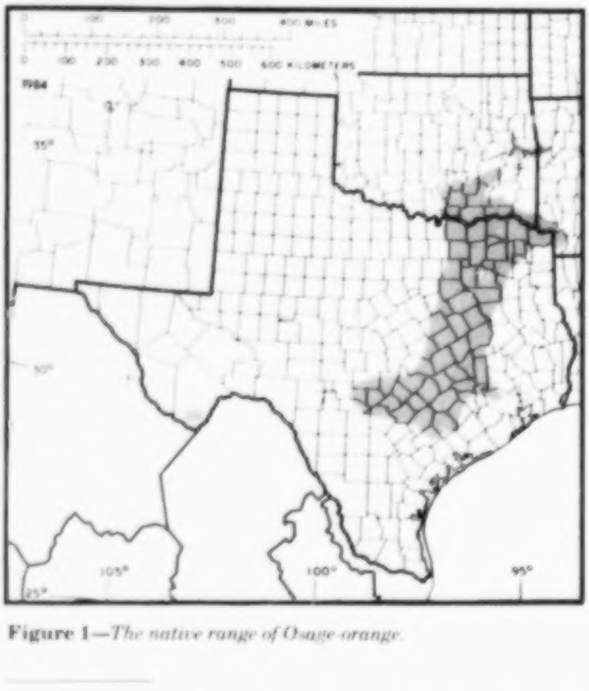

Figure 1—*The native range of Osage-orange.*

Osage-orange has been planted as a hedge in all the 48 conterminous States and in southeastern Canada. The commercial range includes most of the country east of the Rocky Mountains, south of the Platte River and the Great Lakes, excluding the Appalachian Mountains.

Climate

Within the natural range of Osage-orange, average annual temperature ranges from about 18° to 21° C (65° to 70° F), July temperature averages 27° C (80° F) and January temperature ranges from 6° to 7° C (43° to 45° F) with an extreme of -23° C (-10° F). The frost-free period averages 240 days. Average annual precipitation ranges from 1020 to 1140 mm (40 to 45 in), and April to September rainfall from 430 to 630 mm (17 to 25 in).

Osage-orange is hardy as far north as Massachusetts but succumbs to winter-kill in northeastern Colorado and the northern parts of Nebraska, Iowa, and Illinois *(34,36)*.

Soils and Topography

Even within the limited native range, growth of Osage-orange before agricultural settlement was restricted to about 26 000 km² (10,000 mi²), and probably half that area produced no trees of merchantable size *(17,32)*. Some pure stands covered as much as 40 ha (100 acres), but most were much smaller. Pure stands appeared on rich bottom-land soils and were called "bodark swamps" (colloquialism for bois-d'arc). Though not true swamps, these areas frequently became inundated. Over much of its natural range, particularly south of the Red River, Osage-orange grew in isolated small stands, either pure or mixed with other hardwoods, interspersed with prairie. The largest trees and those of the best quality grew on bottom lands of the Red River tributaries in Oklahoma. Most bodark swamps have been converted to fields, and within the Red River system today Osage-orange grows most commonly on sandy terraces not yet occupied by other vegetation and on Blackland Prairie soils underlain by chalk or marl. Distribution and abundance of natural

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regeneration seem to depend more on lack of competition than on kind, quality, or condition of soil.

Osage-orange readily escapes from cultivation and invades exposed, eroding soil, particularly in overgrazed pastures. Thickets are characteristically found along fence rows, ditch banks, ravines, and around abandoned farmsteads.

Most observers report that Osage-orange grows vigorously on all soils *(32,34)*. Some state, however, that hedges planted on soil from which the A1 horizon is removed do not thrive as well as those on less eroded sites *(48)*. On sandy soils where the topsoil was blown away, growth of Osage-orange (and other species) in the Prairie States Forestry Project is strongly retarded *(33)*. Natural regeneration is abundant and vigorous on many soils (Alfisols, Ultisols, Vertisols, and Mollisols), including those too alkaline for most forest trees. The species is sensitive to soil compaction. It thrives best on moist soils but tolerates extreme drought. It is resistant to heat, road salt *(22)*, and urban air pollution *(42)*.

Associated Forest Cover

Osage-orange is not included in any of the forest types recognized by the Society of American Foresters *(13)*. In moist, well-drained minor bottomlands in northwestern Louisiana and nearby parts of Oklahoma, Arkansas, and Texas, it is found with white oak *(Quercus alba)*, hickories *(Carya* spp.), white ash *(Fraxinus americana)*, and red mulberry *(Morus rubra) (37)*. In Nebraska and Kansas, it invades overgrazed pastures, accompanied by honeylocust *(Gleditsia triacanthos)* and is succeeded by black walnut *(Juglans nigra)*, oaks *(Quercus* spp.), hackberry *(Celtis* spp.), hickories, and elms *(Ulmus* spp.) *(18)*. Among the most common associates on limestone-derived soils in middle Tennessee and neighboring portions of Kentucky and Alabama are eastern redcedar *(Juniperus virginiana)*, black walnut, hickories, and elms *(45)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Osage-orange is dioecious. The simple, green, four-part flowers appear soon after the leaves on the same spurs, opening from April through June, and are wind pollinated. Male flowers are long peduncled axillary racemes 2.5 to 3.8 cm (1 to 1.5 in) long on the terminal leaf spur of the previous season; female flowers are in dense globose heads, axillary to the leaves, about 2.5 cm (1 in) in diameter *(2)*. The female flower in ripening becomes very fleshy, forming a large multiple fruit or syncarp (fig. 2) composed of 1-seeded drupelets. The fruit ripens from September through October. The ripe fruit, 7.6 to 15 cm (3 to 6 in) in diameter, yellowish-green, resembles an orange, often weighing more than a kilogram (2.2 lb). Fruits average 23/dkl (80 to the bu) *(53)*. When bruised, the fruit exudes a bitter milky juice which may cause a skin rash and which will blacken the fruit on drying.

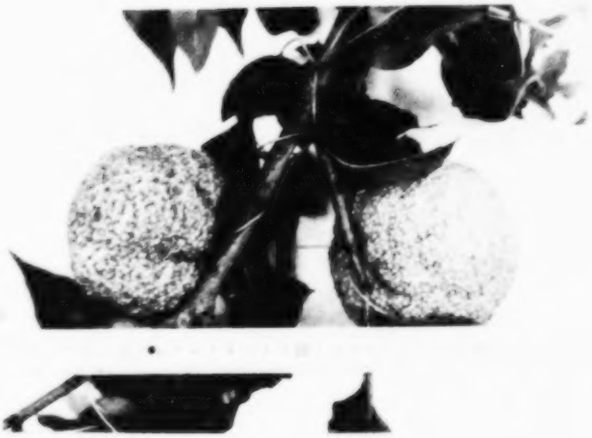

Figure 2—*Ripe fruit of Osage-orange (scale in cm).*

Female trees often produce abundant fruit when no male trees exist nearby, but such fruit contains no seeds.

Seed Production and Dissemination—Female trees bear good seed crops nearly every year, beginning about the 10th year. Commercial seed-bearing age is optimum from 25 to 65 years, and 75 to 100 years may be the maximum *(53)*. Germinative capacity averages 58 percent. Seeds are nearly 1 cm (0.4 in) in length. The number of clean seeds ranges from 15,400 to 35,300, averaging 30,900/kg (7,000 to 16,000, averaging 14,000/lb). Livestock, wild mammals, and birds feed on the fruit and disseminate the seed. The seeds have a slight dormancy that is easily overcome by soaking in water for 48 hours or by stratifying in sand or peat for 30 days. Fruit stored over winter in piles outdoors is easily cleaned in the spring, and the seed germinates promptly. Viability can be maintained for at least 3 years by storing cleaned, air-dried seeds in sealed containers at 5° C (41° F) *(56)*. Recommended sowing depth is about 6 to 13 mm (0.25 to 0.5 in); soil should be firmed.

Seedling Development—Germination is epigeal. Natural regeneration apparently requires exposed mineral soil and full light. A study of survival and growth in the Prairie States Forestry Project windbreaks indicated average survival of Osage-orange at age 7 years to be 68 percent, ranking seventh of 16 "shrubs"; total height was 2.4 m (8 ft), ranking fifth of 16; and crown spread was 1.8 m (6 ft). Osage-orange was usually planted in the shrub (outer) rows and sometimes in the tree (inner) rows. It grows too fast, however, to be considered a shrub and often overtops slower growing conifers *(33)*.

Vegetative Reproduction—Osage-orange may be vegetatively propagated using root cuttings or with greenwood cuttings under glass. To propagate thornless male (nonfruiting) clones for ornamental use, scions or cuttings should be taken only from the mature part of the crown of a tree past the juvenile stage. Perhaps the easiest way to grow selected stock is by grafting chip buds onto nursery-run seedlings and plastic-wrapping the graft area *(30,31)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Osage-orange is a small tree or large shrub averaging 9 m (30 ft) in height at maturity (fig. 3). Isolated trees on good sites may reach heights of as much as 21 m (70 ft); crowded trees usually do not grow so tall. In windbreak plantings on the Great Plains, Osage-orange grew 6 m (20 ft) tall on average sites during a 20-year period; on some sites it grew 12 m (40 ft) tall *(39)*.

Branchlets growing in full sunlight bear sharp, stout thorns. Slow-growing twigs in the shaded portions of the crown of mature trees are thornless. The thorns, 1.3 to 2.5 cm (0.5 to 1 in) long, are modified twigs. They form in leaf axils on 1-year-old twigs (fig. 4). Shade-killed lower branches remain on the tree many years. Regional estimates, based on the 1964-1966 Forest Surveys, indicated virtually no Osage-orange of commercial size and quality on forest land in Oklahoma, Texas, and Louisiana. There are two reasons for this: the species usually grows on nonforest land, and merchantability standards for forest trees do not apply to Osage-orange. Mature trees have short, curved boles and low, wide, deliquescent crowns. Even in closed stands on good sites, less than half the stems contain a straight log, 3 m (10 ft) long, sound and free of shake.

Rooting Habit—Osage-orange is characteristically deep rooted, but because it has been planted so widely, the species is usually off site, where its rooting habit is variable. When the tree grows on shallow, fertile soils over limestone, the lateral rootspread is tremendous *(32)*.

Excavation of root systems in 7-year-old or older shelterbelts revealed a lateral radius of 4.3 m (14 ft) and a depth of more than 8.2 m (27 ft) for Osage-orange near Goodwell, OK *(9)*. The soil was Richfield silt loam. Most of the lateral roots were in the uppermost 0.3 m (1 ft) of soil. Excavations in Nebraska revealed a lateral radius of 2.1 m (7 ft) and a depth of 1.5 m (5 ft) for 3-year-old Osage-orange in Wabash silt loam; for 23-year-old Osage-orange in Sogn silty clay loam, lateral radius was 4.9 m (16 ft) and depth was 2.4 m (8 ft) *(47)*. At both ages, there was a well-developed taproot, and most of the long laterals

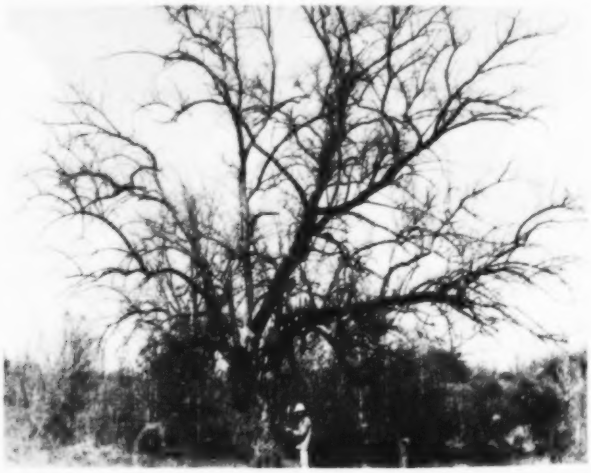

Figure 3—*Mature Osage-orange tree 66 cm (26 in) in d.b.h. and 14.6 m (48 ft) in total height, near Bastrop, LA.*

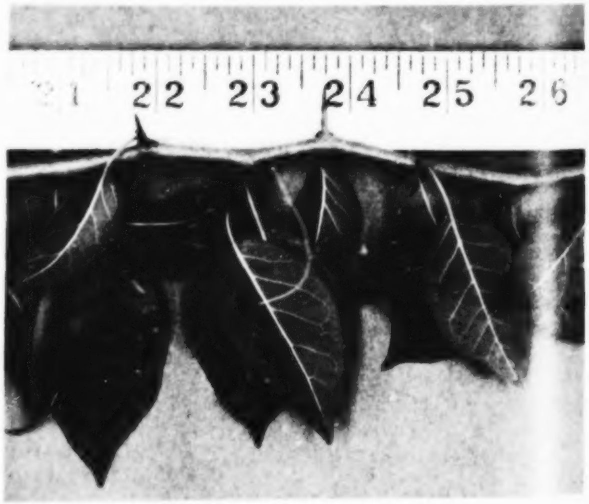

Figure 4—*Thorns in leaf axils on fast-growing 1-year-old shoots of Osage-orange in full sunlight (scale in inches).*

originated within the first 0.3 m (1 ft) of soil. At 3 years, most of the long laterals were within the first 0.6 m (2 ft) of soil; at 23 years, laterals were as abundant in the eighth as in the first foot of soil.

Reaction to Competition—Osage-orange is tolerant according to some authors *(6,37)* and very intolerant according to others *(3)*. Overall, it is most accurately classed as intolerant of shade. The occurrence and circumstances of natural regeneration suggest intolerance, but the growth of planted Osage-orange in hedges and shelterbelts, under strong competition, indicates tolerance. How vigorously and at how advanced an age the species responds to release has not been determined. Severe competition does not prevent abundant seed production. Osage-orange sprouts vigorously, even following cutting of interior rows in windbreaks.

No literature on the silviculture of naturally regenerated forest stands of Osage-orange is known.

Damaging Agents—Although Osage-orange is one of the healthiest tree species in North America, it is attacked by some parasites. Cotton root rot, caused by *Phymatotrichum omnivorum*, attacks Osage-orange and most other windbreak species in Texas, Oklahoma, and Arizona *(59)*. Losses are greatest in plantings on dry soil where rainfall is scant. Cotton root rot is the only serious disease.

Two species of mistletoe, *Phoradendron serotinum* and *P. tomentosum*, grow in the branches and cause witches' brooms. Osage-orange ornamentals in the Northeast have occasionally succumbed to Verticillium wilt, caused by *Verticillium albo-atrum*. Leafspot diseases are caused by *Ovularia maclurae, Phyllosticta maclurae, Sporodesmium maclurae, Septoria angustissima, Cercospora maclurae,* and *Cerotelium fici*. Seedlings in a Nebraska nursery have been killed by damping-off and root rot caused by *Phythium ultimum* and *Rhizoctonia solani (21)*. *Phellinus ribis* attacks stemwood exposed in wounds. *Poria ferruginosa* and *P. punctata* are the only two wood-destroying basidiomycetes reported on Osage-orange; they occur only on dead wood, mainly in tropical and subtropical parts of the western hemisphere *(21)*. Maclura mosaic virus and cucumber mosaic virus have been identified in leaf tissue of Osage-orange in Yugoslavia *(35)*.

Osage-orange trees are attacked by at least four stem borers: the mulberry borers *(Doraschema wildii* and *D. alternatum) (4)*, the painted hickory borer *(Megacyllene caryae)*, and the red-shouldered hickory borer *(Xylobiops basilaris) (8)*. The twigs are parasitized by several scale insects including the European fruit lecanium *(Parthenolecanium corni)*, the walnut scale *(Quadraspidiotus juglansregiae)*, the cottony maple scale *(Pulvinaria innumerabilis)*, the terrapin scale *(Mesolecanium nigrofasciatum)*, and the San Jose scale *(Quadraspidiotus perniciosus) (25,46)*. The fruit-tree leafroller *(Archips argyrospilus)* feeds on opening buds and unfolding leaves.

Osage-orange is attacked by, but is not a principal host of, the fall webworm *(Hyphantria cunea) (55)*, an Eriophyid mite, *Tegolophus spongiosus (51)*, and the fourspotted spider mite, *Tetranychus canadensis (4)*.

Osage-orange trees and several other species in 1- to 5-year-old plantations on old fields in the prairie region of Illinois were partially or completely girdled by mice. Severity of damage was greatest where weeds were most abundant *(26)*.

Windbreaks on the Great Plains, unless given cultivation during their early years, are invaded by herbaceous vegetation, become sod bound, and are permanently damaged *(33,38,39)*. This vegetation may harbor rodents. Grazing is not satisfactory for herbage control; multiple-row windbreaks should be fenced to exclude livestock.

Osage-orange sustained less damage by insects, diseases, drought, hail, and glaze than any other species planted in the Prairie States Forestry Project. Along with bur oak *(Quercus macrocarpa)* it survived better than any other deciduous species on uplands of the Southern Plains *(7,38)*.

Special Uses

Osage-orange has been planted in great numbers, first as a field hedge, before barbed wire became available, secondly as a windbreak and component of shelterbelts, and thirdly to stabilize soils and control erosion.

The single-row field hedge proved to be a valuable windbreak on the prairie; evidence of this was the raised ground level under 15-year-old hedges, caused by accumulation of windborne soil material. Hedges around every quarter-section were common, especially in areas of deep sand *(20,38)*. These hedges were a source of durable posts. Prairie farmers customarily clearcut hedges on a 10- to 16-year cycle, obtaining about 2,500 fence posts per kilometer (4,000 per mi) of single-row hedge. The slash was piled over the stumps to protect the new sprouts from browsing livestock. Pole-sized and larger Osage-orange trees are practically immune to browsing, but seedlings and tender sprouts are highly susceptible. Recommended practice is to thin the new sprout stands to 240 vigorous stems per 100 m (73/100 ft), 3 to 5 years after the clearcut, and to protect the sprouts from fire. If inadvertently burned, the sprouts should be cut back immediately to encourage new, vigorous growth *(20)*.

Osage-orange heartwood is the most decay-resistant of all North American timbers and is immune to termites. The outer layer of sapwood is very thin; consequently, even small-diameter stems give long service as stakes and posts *(40,43)*. About 3 million posts were sold annually in Kansas during the early 1970's. The branch wood was used by the Osage Indians for making bows and is still recommended by some archers today.

The chemical properties of the fruit, seed, roots, bark, and wood may be more important than the structural qualities of the wood. A number of extractives have been identified by researchers, but they have not yet been employed by industry *(11,12,23, 24,44,58)*. Numerous organic compounds have also been obtained from various parts of the tree *(16,44,57)*. An antifungal agent and a nontoxic antibiotic useful as a food preservative have been extracted from the heartwood *(5,24)*.

Osage-orange in prairie regions provides valuable cover and nesting sites for quail, pheasant, other birds, and animals *(20,33)*, but the bitter-tasting fruit is little eaten by wildlife. Reports that fruit causes the death of livestock have been proven wrong by feeding experiments in several States.

Osage-orange has been successfully used in strip mine reclamation. Its ease of planting, tolerance of alkaline soil, and resistance to drought are desirable qualities *(1,14,29)*. These qualities plus growth, long life, and resistance to injury by ice, wind, insects, and diseases make Osage-orange a valued landscape plant *(15,30,31)*.

Genetics

There is no known literature on the genetics of Osage-orange, and no information on geographic races is available. A thornless cultivar, *Maclura pomifera* var. *inermis* (André) Schneid., can be propagated by cuttings or scions taken from high in the crowns of old trees, where the twigs are thornless *(30,31)*. The only known hybrid, × *Macludrania hybrida* André, is an intergeneric cross: × *Macludrania* = *Cudrania* × *Maclura*. *Cudrania tricuspidata* (Carr.) Bureau is a spiny shrub or small tree, native to China, Japan, and Korea. The *Maclura* parent is variety *inermis*. The hybrid is a small tree with yellowish furrowed bark and short, woody spines *(2,41)*. Some authorities believe that the tropical dye-wood, fustic &*Chlorophora tinctoria* (L.) Gaud.é belongs in the genus *Maclura*; however, the majority opinion is that there is only one species of Osage-orange *(28)*.

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Magnolia acuminata L. Cucumbertree

Magnoliaceae Magnolia family

H. Clay Smith

Cucumbertree (*Magnolia acuminata*), also called cucumber magnolia, yellow cucumbertree, yellow-flower magnolia, and mountain magnolia, is the most widespread and hardiest of the eight native magnolia species in the United States, and the only magnolia native to Canada. They reach their greatest size in moist soils of slopes and valleys in the mixed hardwood forests of the southern Appalachian Mountains. Growth is fairly rapid and maturity is reached in 80 to 120 years. The soft, durable, straight-grained wood is similar to yellow-poplar (*Liriodendron tulipifera*). They are often marketed together and

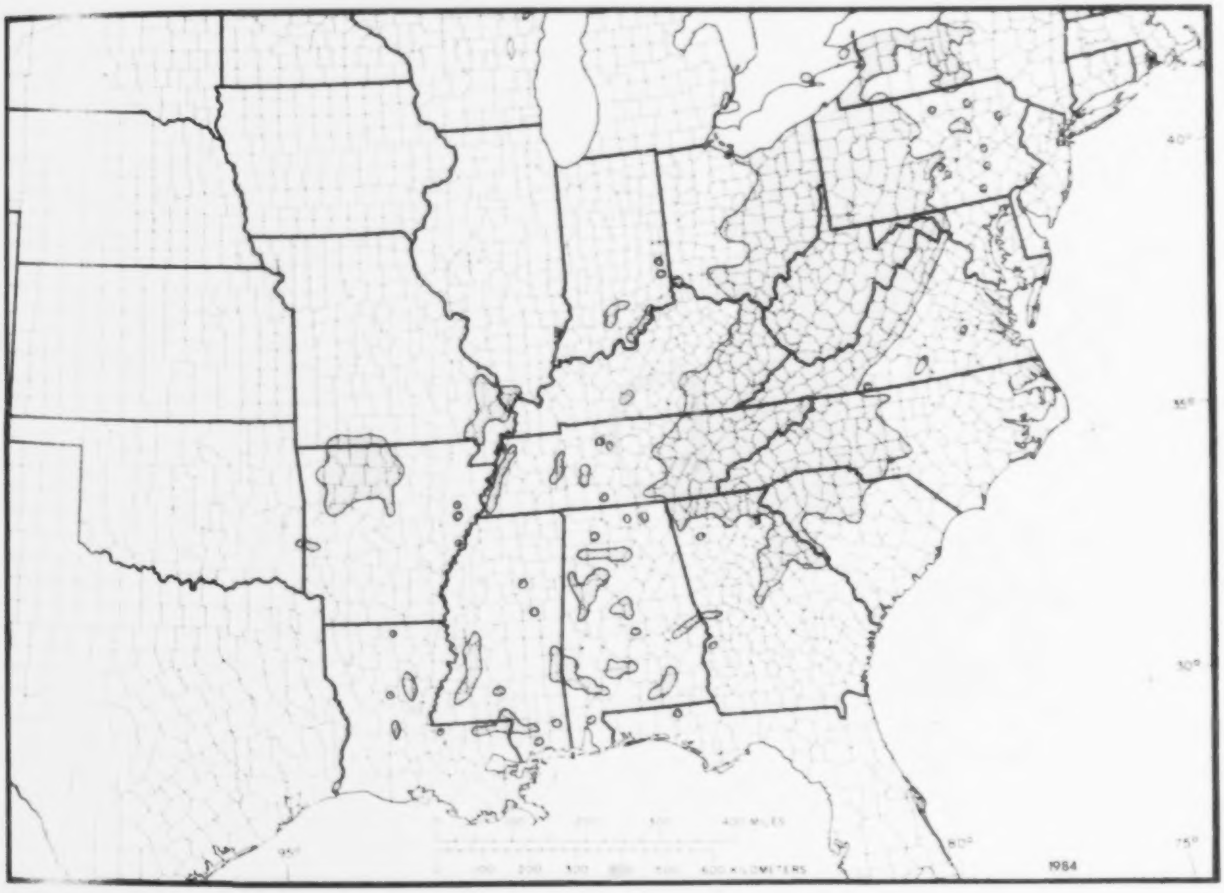

Figure 1—*The native range of cucumbertree*

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used for pallets, crates, furniture, plywood, and special products. The seeds are eaten by birds and rodents and this tree is suitable for planting in parks.

Habitat

Native Range

Cucumbertree (figs. 1, 2) is widely distributed but never abundant. It grows on cool moist sites mostly in the mountains from western New York and southern Ontario southwest to Ohio, southern Indiana and Illinois, southern Missouri south to southeastern Oklahoma and Louisiana; east to northwest Florida and central Georgia; and north in the mountains to Pennsylvania.

Climate

Cucumbertree is the hardiest of the native tree-size magnolias. The climate is described as humid to subhumid throughout its range. There are 110 to 260 days in the growing season, with 150 to 160 frost-free days in the northern portion of the range and 180 to 230 frost-free days in the southern portion. Annual precipitation measures 890 to 2030 mm (35 to 80 in), of which about 510 to 1020 mm (20 to 40 in) fall during the growing season. The mean annual temperature varies from a low of 7° C (45° F) in the northern range to 18° C (65° F) in the south. January temperatures usually are between -7° to 10° C (20° to 50° F); July temperatures are between 18° to 27° C (65° to 80° F); however, sometimes there are extremes well above and well below these temperatures for relatively short periods of time. Average annual snowfall measures from 200 cm (80 in) or more in the north to only a trace of snow in the south *(25,29)*.

Soils and Topography

This species prefers rich soils of bottomland and north to east slopes and is most plentiful in mountains and hills. The soils must be well drained, moist, and deep. Most slopes where this species is found are gentle to moderate, up to 25 percent, though cucumber tree is also found on steeper slopes. The species is found at elevations as high as 1524 m (5,000 ft) above sea level.

Cucumbertree is found in three orders and five suborders of soil *(28)*. The dominant order, Inceptisols, occurs on approximately 60 percent of the species range, particularly in the Appalachians. On steep slopes greater than 25 percent, cucumbertree

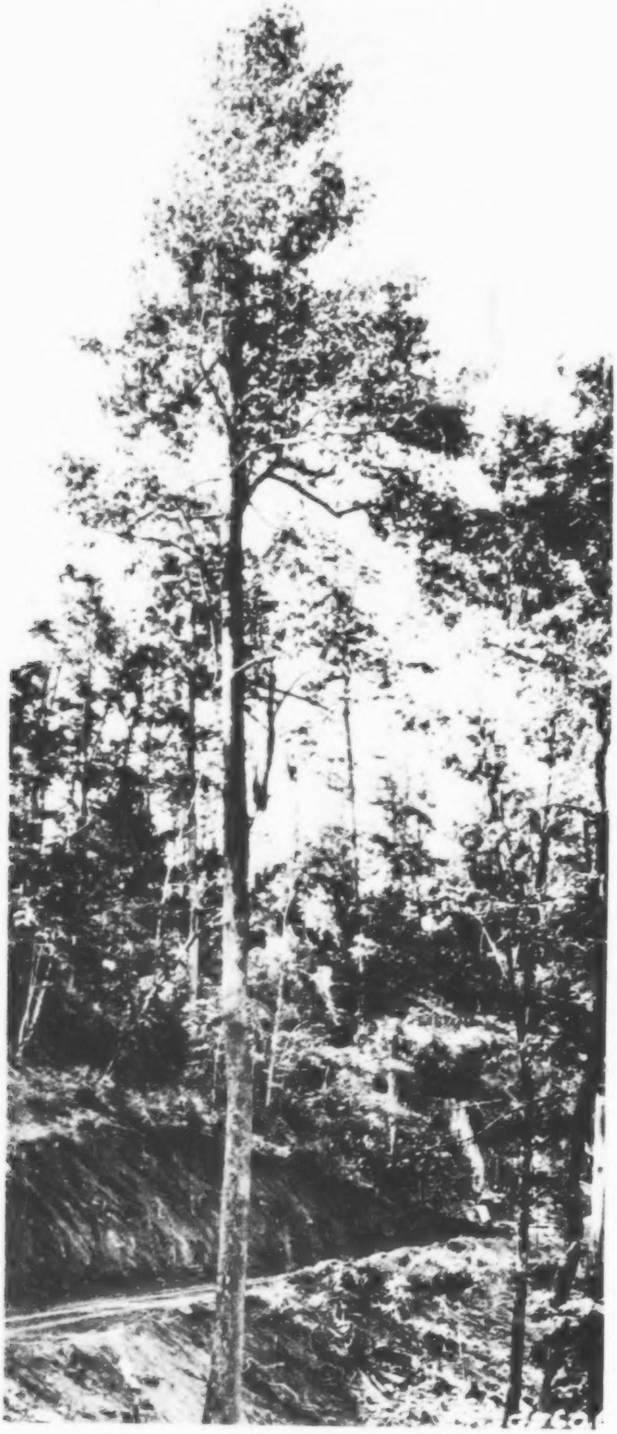

Figure 2—*Cucumbertree in the Pisgah National Forest, NC*

grows on coarse loams. On gentle to moderate slopes it is found on fine loams. Here, water is readily available to plants during more than one-half of the year or more than three consecutive months during the growing season. Soil textures are finer than loamy sand and these soils have a moderate to high nutrient content.

Approximately 35 percent of the soils are Ultisols, occurring on gentle to steep slopes in the southern range. These soils are low in nutrients. On slopes greater than 25 percent, cucumbertree grows on fine to coarse loams, clays, and on well-drained quartz sands. On slopes up to 25 percent it is confined to coarse loams *(28)*.

The remaining soils on which cucumbertree grows are in the order Alfisols.

Associated Forest Cover

Cucumbertree is found scattered in the oak-hickory forest. It is an associated species in six eastern intermediate to climax forest cover types *(5)*. In northern hardwoods cucumbertree is a minor component in Sugar Maple (Society of American Foresters Type 27) and Black Cherry–Maple (Type 28). In upland oaks of the central forest region it is a component in White Oak–Black Oak–Northern Red Oak (Type 52), Yellow-Poplar (Type 57), Yellow-Poplar–Eastern Hemlock (Type 58), and Yellow-Poplar–White Oak–Northern Red Oak (Type 59).

In the northern and central hardwoods and Appalachian Highlands, cucumbertree commonly is associated with sugar maple *(Acer saccharum)*, yellow-poplar *(Liriodendron tulipifera)*, yellow buckeye *(Aesculus octandra)*, several oaks *(Quercus* spp.), and black walnut *(Juglans nigra)*. Common understory vegetation includes spring beauty *(Claytonia caroliniana)*, trilliums *(Trillium* spp.), violets *(Viola* spp.), Solomons-seal *(Polygonatum pubescens)*, and sweet cicely *(Osmorhiza* spp.). In the Allegheny Plateau of northern Pennsylvania and southern New York, cucumbertree usually is associated with black cherry *(Prunus serotina)*, sugar maple, yellow birch *(Betula alleghaniensis)*, sweet birch *(B. lenta)*, yellow-poplar, hemlock *(Tsuga* spp.), basswood *(Tilia* spp.), northern red oak *(Quercus rubra)*, and butternut *(Juglans cinerea)*. Understory vegetation includes black cherry, white ash *(Fraxinus americana)*, sugar maple, beech *(Fagus grandifolia)*, red maple *(Acer rubrum)*, striped maple *(A. pensylvanicum)*, witch-hazel *(Hamamelis virginiana)*, hobblebush *(Viburnum alnifolium)*, and other viburnums.

In the upland oak types throughout the East, cucumbertree is associated with white oak *(Quercus alba)*, red oak, black oak *(Q. velutina)*, chestnut oak *(Q. prinus)*, yellow-poplar, elms *(Ulmus* spp.), hickories *(Carya* spp.), maples, blackgum *(Nyssa sylvatica)*, white ash, basswood, yellow birch, and black cherry. Common understory species include dogwood *(Cornus* spp.), sassafras *(Sassafras albidum)*, sourwood *(Oxydendrum arboreum)*, serviceberry *(Amelanchier arborea)*, viburnums, witch-hazel, grape *(Vitis* spp.), greenbrier *(Smilax* spp.), tick trefoil *(Desmodium* spp.), and hawthorn *(Crataegus* spp.).

In the Appalachian and Cumberland Mountains, cucumbertree commonly occurs with yellow-poplar, eastern hemlock *(Tsuga canadensis)*, white ash, basswood, birches, sugar maple, northern red oak, black oak, and white oak. Common understory vegetation includes hemlock, sugar maple, beech, birch, rhododendron *(Rhododendron* spp.), viburnums, wild hydrangea *(Hydrangea arborescens)*, and several ferns *(Dyopteris* spp.). At higher elevations in the central uplands oak types, cucumbertree is associated with yellow-poplar, white oak, northern red oak, black cherry, buckeye, white ash, beech, eastern white pine *(Pinus strobus)*, and maples. Understory vegetation includes maples, oaks, hickory, black cherry, grape, spicebush *(Lindera benzoin)*, wild hydrangea, viburnum, dogwood, and ferns.

At its southern limits in the Coastal Plains from Louisiana to west Florida, cucumbertree is associated with Sweetbay *(Magnolia virginiana)*, bigleaf magnolia *(M. macrophylla)*, and southern magnolia *(M. grandiflora)* in addition to white oak, water oak *(Quercus nigra)*, swamp chestnut oak *(Q. michauxii)*, and southern red oak *(Q. falcata)*, elms, hickories, yellow-poplar, beech, maples, white ash, and blackgum.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Cucumbertree flowers from early April through early July depending on location *(22)*. Self-pollination usually does not occur because the flowers do not produce ripe pollen until the female stigma is no longer receptive *(12)*. Magnolia flowers are perfect and are borne singly at the ends of the branches. They appear after the leaves start developing. The flowers close at night and do not last longer than 2 to 4 days. Pollination is largely by insects. The fruit, a green cucumber-shaped cone, ripens in late August or September. The thickened, rounded, red knobby follicles open exposing reddish-orange seeds that hang on slender threads before falling to the ground *(7)*. The outer seedcoat is fleshy, oily, and soft; the inner seedcoat is hard, thin, and membranous enclosing a large and fleshy endosperm.

Weather adversely influences the sensitive flower receptivity and available pollen. Also, cucumbertrees have a shorter period of receptivity and pollen shedding than other native magnolias *(14)*.

Seed Production and Dissemination—Cucumbertree produces from 10 to 60 seeds per fruit. Good seed crops usually occur every 4 to 5 years, but less frequently at the margins of the geographic range. Light seed crops occur in intervening years. Seed bearing begins at about 30 years and is optimum at age 50 and beyond *(18)*. The average number of uncleaned seeds per kilogram is about 3,530 (1,600/lb); for depulped, cleaned seed, the average ranges from about 6,400 to 14,600/kg (2,900 to 6,600/lb) *(7,18)*. Seeds are usually disseminated by birds, wind, water, and gravity soon after ripening in the fall.

Seedling Development—Magnolia seed of all species seems more sensitive to adverse temperatures and moisture factors than other tree seed *(7)*. All seeds of magnolia species lose viability if fully dried or stored over winters at room temperatures. During germination, the cotyledons (epigeous) emerge from the ground. Germination occurs the first or second spring following seed production. Seed dormancy can be overcome by several months of low temperature. Normally, it is essential to stratify the seed for first-year germination. Moist, cold storage is recommended *(14)*. Average seed germination is 55 percent; seeds germinate in 35 to 60 days. The clean or uncleaned seed can be stored at 0° to 5° C (32° to 41° F) in sealed containers for several years with little loss of viability.

Reproduction of cucumbertree in the forests is scarce because of the destruction of seeds by birds and rodents, high susceptibility of the seedlings to freezing, and the exacting conditions required for germination *(18)*. Nursery practices used to artificially propagate magnolia seed include sowing the seed in the fall or stratifying the seed several months and then sowing the seed in the late winter or spring. The beds should be mulched and the mulch not removed until there is no possibility of a late spring frost. Young seedlings need half shade during most of the first summer in the seedbed. Normally plantings are done with 1-0 bare root seedlings *(18)*. Cucumbertree is easy to transplant *(30)*.

Vegetative Reproduction—Cucumbertree sprouts readily and often is used as grafting root stock for named varieties and ornamental species. Propagation is from seed or grafts; use of cuttings is unsuccessful *(15)*. Successful grafting allows this species to be grown far north of its natural range *(17)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Cucumbertree can reach a height of about 30 m (100 ft) and a d.b.h. of 91 to 122 cm (36 to 48 in). Typically, this tree is 18 to 24 m (60 to 80 ft) tall and 60 cm (24 in) in d.b.h. Cucumbertree grows fast in moist, deep soils of coves and lower slopes. This species matures in 100 years and seldom lives more than 150 years *(8)*. Generally, the species is rapid growing and short lived. There are no available published data on the growth rate and yield of individual trees.

Rooting Habit—The root system for cucumbertree is deep and widespread, and trees rarely develop a taproot *(30)*. Cucumbertree is susceptible to windthrow, especially on steep slopes.

Reaction to Competition—This species is classed as intermediate in shade tolerance *(24)*. Observations on the Fernow Experimental Forest, Parsons, WV, indicate that cucumbertree regeneration is more frequent in clearcuts than in partial cuts. In early development of central Appalachian hardwood stands, cucumbertree competes favorably with yellow-poplar and black cherry on good oak sites and with oak species on fair sites. Cucumbertree is similiar to yellow-poplar in that it usually develops a straight bole at a young age. Cucumbertree produces considerable branches, but since it self-prunes well in closed stands, it is usually clear boled *(8)*.

Damaging Agents—Cucumbertree has no important disease agents; however, it is very sensitive to ground fires and frost *(8)*. *Nectria galligena* is common on cucumbertree stands on unsuitable sites, particularly in the southern Appalachian region. *Nectria* cankers cause defects but seldom kill the tree.

Ambrosia beetles such as *Platypus compositus*, a common wood borer, seriously degrade recently felled trees during warm months. In the South, it is common to saw logs within 2 to 3 weeks after felling *(2)*. The magnolia scale *(Neolecanium cornuparvum)*, one of the largest scale insects in the United States, can seriously injure magnolia species. Other sap-sucking insects that attack cucumbertree are the European fruit lecanium *(Parthenolecanium corni)*, the oleander pit scale *(Asterolecanium pustulans)*, and the San Jose scale *(Quadraspidiotus perniciosus)*. Common insect defoliators of cucumbertree are

Odontopus calceatus, Phyllocnistis magnoliella, **and *Phyllophaga forsteri (2).***

Sapsucker damage is common on cucumbertree. Bird peck causes stain streaks in the wood several feet above and below each peck, resulting in lumber degrade.

Special Uses

In general, wildlife use of cucumbertree for food is low; however, the seeds are eaten by several species of birds and small mammals *(11)*. Grackles and blackbirds also eat the young fruit of the cucumber tree *(14)*. Twigs, leaves, and buds are browsed by deer, although cucumbertree is classed as nonpalatable by some investigators *(9)*, others have considered it an important deer plant food in West Virginia during one or more seasons *(1)*.

Cucumbertree is a valuable forest and shade tree, highly desirable for ornamental planting because of the showy flowers, fruits, and attractive foliage and bark *(18)*. This species has been planted successfully well north of its native range *(4)*; it grows well in slightly acid, well-drained soil *(26)*.

Cucumbertree is used for wood products and resembles yellow-poplar except that the wood is heavier, harder, and stronger *(3)*. This species is commonly used for lumber in the Appalachian Mountains, especially in West Virginia and adjoining States. The wood is usually sold as yellow-poplar; it has not been sold as cucumbertree lumber since 1928 *(3)*. The wood is used in furniture, fixtures, venetian blinds, siding, interior trim, sashes, doors, boxes, and crates *(10)*. Cucumbertree is not as desirable for fuelwood as the denser hardwoods. Compared with hickory, which has a fuel value of 100, cucumbertree has a fuel value of 57 (on a volume basis).

Cucumbertree has a specific gravity of 0.44 based on oven-dry weight and green volume, and 0.48 based on oven-dry weight and volume at 12 percent moisture content *(27)*. Generally, the wood is close grained, durable, and susceptible to decay. Sapwood typically is a light color while the heartwood is pale brown. The branches of this species are soft and break easily, making tree climbing difficult *(22)*.

Genetics

Population Differences

The magnolia genus is one of the most ancient among flowering trees. Though subgenera may be intergrafted, pollinations across subgenetic divisions have yielded only apomicts of the female parent *(13)*. Cucumbertree is tetraploid and is the only American species of subgenus *Yulania*.

Races and Hybrids

Most of the variability of the species is in the southern part of its range *(17)*. Geographic varieties of cucumbertree include *Magnolia acuminata* var. *cordata* in the Piedmont; var. *ozarkensis* in the Ouachita and Ozark Mountains; var. *acuminata* over the range except for the Piedmont; *M. acuminata* forma *aurea* in the mountains and upper Piedmont of North and South Carolina, Georgia, and Tennessee; and *M. acuminata* var. *alabamensis* and *M. acuminata* var. *subcordata* in the Piedmont and Coastal Plain *(6,20,21)*.

Cucumbertree is used successfully as root stocks, for chip-budding, and in other grafting methods with *Magnolia macrophylla*. Factors complicate hybridization possibilities. This species is the latest of the subgenus *Yulania* to open its flower in the spring. Some successful hybrids include "Woodsman" (*M. acuminata* × *liliflora*) called *Magnolia* × *brooklynensis*. There have been successful crosses of *Magnolia acuminata* with *M.* × *brooklynensis* and *M.* × *soulangiana*. A hybrid has been developed from *M. acuminata* × *sprengeri*. If the possibility of a spring frost is great, newly developed hybrids may not flower *(13,15,16,20,21)*. Natural crosses of *M. acuminata* and *M. denudata* seldom occur *(19)*. Artificial hybrids with other species are possible in the subgenus *Yulania*. Several successful additional combinations of hybrid crosses have been noted *(23)*.

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Magnolia fraseri Walt. Fraser Magnolia

Magnoliaceae Magnolia family

Lino Della-Bianca

Fraser magnolia (*Magnolia fraseri*), also called mountain magnolia, earleaf cucumbertree, umbrella-tree, or mountain-oread, is a fast-growing small tree scattered in the hardwood forests of the lower Appalachian slopes. It grows best on rich, moist, well-drained soils. The very large showy white flowers and large coarse foliage make this an attractive ornamental; otherwise it has little commercial value. The lumber is mixed with associated hardwoods for sawtimber and pulpwood, and the fruit is eaten by wildlife (*9,16*).

Habitat

Native Range

Restricted mostly to the Appalachians, Fraser magnolia (fig. 1) is found in moist habitats in the

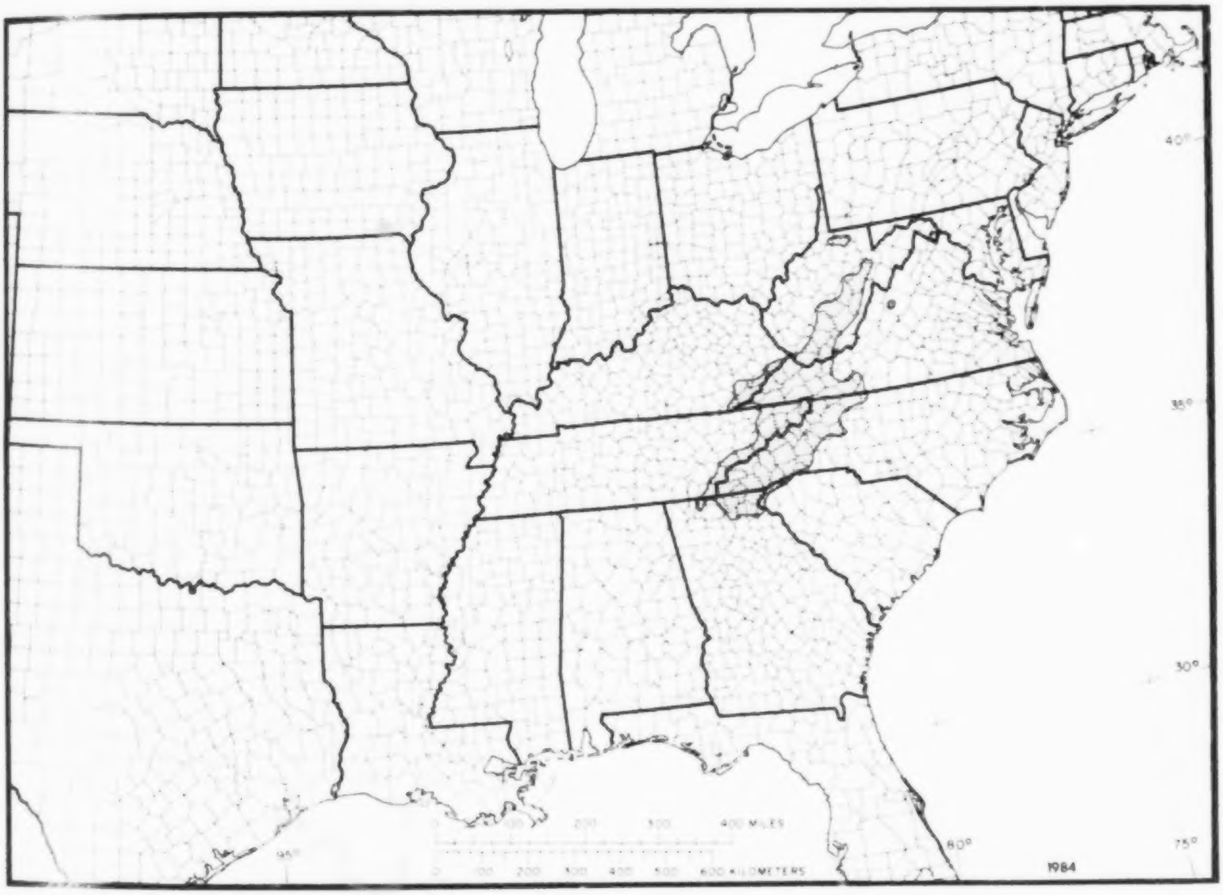

Figure 1—*The native range of Fraser magnolia.*

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mountains of West Virginia, generally in the eastern half of the State, in western Virginia, in the southern Appalachians of east Tennessee and western North Carolina, and in the Blue Ridge Mountains of northwestern South Carolina and northeast Georgia *(12,13)*. It also grows in the Cumberland Mountains of southeastern Kentucky.

Climate

Within the natural range of Fraser magnolia during the growing season, average rainfall varies considerably. In West Virginia, April to September rainfall averages 610 to 760 mm (24 to 30 in), but in north Georgia and western North Carolina, it averages 910 to 990 mm (36 to 39 in) *(17)*. Total annual precipitation in West Virginia varies from 1020 to 1270 mm (40 to 50 in), while in the southern Appalachians, the variation is between 1020 and 2030 mm (40 to 80 in).

July temperatures average 21° to 24° C (70° to 75° F) and January temperatures range from -1° to 2° C (30° to 35° F) where Fraser magnolia occurs in West Virginia and Virginia, and from 2° to 4° C (35° to 40° F) in the southern end of the Appalachians. The frost-free period varies from 150 to 170 days in West Virginia and Virginia, and from 170 to 180 days in the southern Appalachians of eastern Tennessee and western North Carolina.

Soils and Topography

Fraser magnolia is generally found on mesic sites, but seedlings and saplings have been reported to occur on subxeric and even on xeric sites *(4,8,14,15,21)*. In the gorges of the southern Blue Ridge Front, it is more frequently found below midslope, being most common on the lowest third of north and south slopes, and on the bottom land. In the gorge region it has an unusual habit of growing in a multiple-stemmed group on bottoms and as a single-stemmed tree on slopes; elsewhere it occurs in either form. Sites on which it grows best are generally protected, moist, and fertile; soil temperatures on such sites are generally cool during the growing season in comparison with sites farther upslope.

On lower slopes and in the bottom of the Long Spur River Gorge in the southeastern escarpment of the Blue Ridge Mountains between Rosman and Highlands, NC, average chemical contents and other properties of the 0 to 13 cm (0 to 5 in) soil layer of the Tusquitee loam (an Umbric Dystrochrept of the order Inceptisols) supporting Fraser magnolia were as follows: sodium, 0.9 meq/100 g; potassium, 0.20 meq/100 g; calcium, 0.10 meq/100 g; and magnesium, 0.11 meq/100 g; nitrous nitrogen, 1.6 p/m; phosphorus, 2.0 p/m; and iron, 1.9 p/m; pH 4.8; and organic matter, 6.6 percent *(14,20)*. The nutrient status of this soil is low because plentiful soil moisture makes nutrients quickly available to all plants, and the nutrients are thus tied up until the plants are recycled.

In the Great Craggy Mountains above Dillingham, NC, at an elevation of 1200 m (3,940 ft) where the northwest slope averages 40 percent, the following average soil values prevail in a stand composed mostly of sugar maple *(Acer saccharum)*, American beech *(Fagus grandifolia)*, yellow buckeye *(Aesculus octandra)*, and Carolina basswood *(Tilia caroliniana)*, and some Fraser magnolia: pH 4.8, organic matter 7 percent, bulk density 0.96 g/cm^3 (59.9 lb/ft^3). The top 15 cm (6 in) of mineral soil contained phosphate-phosphorus 1.7 kg/ha (1.5 lb/acre), potassium 118 kg/ha (105 lb/acre), calcium 936 kg/ha (835 lb/acre), and magnesium 108 kg/ha (96 lb/acre) *(6)*. The soils are mostly Edneyville stony loam which is a mesic Typic Hapludult of the order Ultisols *(20)*; parent materials are Precambrian acid crystalline rocks, including gneisses, schists, granite, diorite, and some mica-gneisses and mica-schists.

Farther northeast, near Grandfather Mountain (1956 m or 6,417 ft) in the Blue Ridge Front, Fraser magnolia grows on Ashe soil, a Typic Dystrochrept derived from Cranberry granite at an elevation of about 1200 m (3,940 ft). The terrain slopes steeply to the southeast, and the soils are deep, coarse, conspicuously gray–white sandy loams or loams which are very well drained. Rainfall is well distributed and plentiful throughout the year so soil moisture is ample and not restrictive to forest growth.

On the Jefferson National Forest in western Virginia, Fraser magnolia is found mostly on soils developed from sandstone or shale. In the Appalachian Plateau of West Virginia, it grows on rich, moist, colluvial soils derived from upper-Devonian and Pennsylvanian rock formations *(3,7)*. Fraser magnolia generally grows at elevations ranging from 500 to 1700 m (1,640 to 5,580 ft) but is most common from about 600 to 1300 m (1,970 to 4,270 ft).

Associated Forest Cover

Fraser magnolia is a moderately frequent tree species in a number of forest types; however, its relative density is generally less than 10 percent, regardless of its size or location *(3,7,8)*. For example, it constitutes only 0.3 percent of all trees on the Jefferson National Forest in western Virginia.

At elevations greater than 1200 m (3,940 ft) associated species include mountain maple *(Acer* *spicatum*), striped maple (*A. pensylvanicum*), and sugar maple, American beech, American basswood (*Tilia americana*), Carolina basswood, yellow buckeye, yellow birch (*Betula alleghaniensis*), and eastern hophornbeam (*Ostrya virginiana*) (*2,3,4,6,8*). Elsewhere commonly associated species are: sweet birch (*Betula lenta*), hickories (*Carya* spp.), American chestnut (*Castanea dentata*) (as sprouts), flowering dogwood (*Cornus florida*), white ash (*Fraxinus americana*), Carolina silverbell (*Halesia carolina*), American holly (*Ilex opaca*), butternut (*Juglans cinerea*), black walnut (*J. nigra*), yellow-poplar (*Liriodendron tulipifera*), cucumbertree (*Magnolia acuminata*), blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), black cherry (*Prunus serotina*), white, scarlet, chestnut, and northern red oaks (*Quercus alba, Q. coccinea, Q. prinus,* and *Q. rubra*, respectively), black locust (*Robinia pseudoacacia*), white basswood (*Tilia heterophylla*), and eastern hemlock (*Tsuga canadensis*) (*14,15*). Eastern white pine (*Pinus strobus*), pitch pine (*P. rigida*), Table Mountain pine (*P. pungens*), and shortleaf pine (*P. echinata*) are occasional associates.

Life History

Reproduction and Early Growth

Any forest activity that increases the amount of incident light striking the forest floor and exposes mineral soil is conducive to the establishment of Fraser magnolia regeneration on mesic sites that have seed-bearing trees of the species.

Flowering and Fruiting—Fraser magnolia has perfect flowers. The blossoms open from May to June depending on latitude, elevation, and weather conditions. The solitary flowers are about 20 to 30 cm (8 to 12 in) wide; they consist of six to nine obovate-spatulate petals conspicuously constricted below the middle (*9,16*). The fruit is an oblong, conelike aggregate of fleshy one- or two-seeded follicles, that ripen in late summer to early fall. At maturity, the red, drupelike seeds are about 1.5 cm (0.6 in) long.

Seed Production and Dissemination—A good seed crop occurs only every 4 to 5 years. Cleaned seeds range from 5,470 to 12,460/kg (2,480 to 5,650/lb), averaging 10,030/kg (4,550/lb) (*14,18*).

Seedling Development—Germination is epigeal. Stratified seeds placed in a sandy medium and kept at day and night temperatures of 30° C (86° F) and 20° C (68° F), respectively, from 40 to 100 days, have a germinative capacity of 8 to 21 percent—low in comparison to other magnolias (*18*). In spite of low germinative capacity, Fraser magnolia is one of the tree species that colonizes canopy gaps caused by the fall of single, large eastern hemlocks in the Great Smoky Mountains (*2*). It is also common as volunteer regeneration along logging roads in the southern Appalachians and is found frequently as seedlings and saplings in small openings on mesic sites near seed-bearing trees (fig. 2).

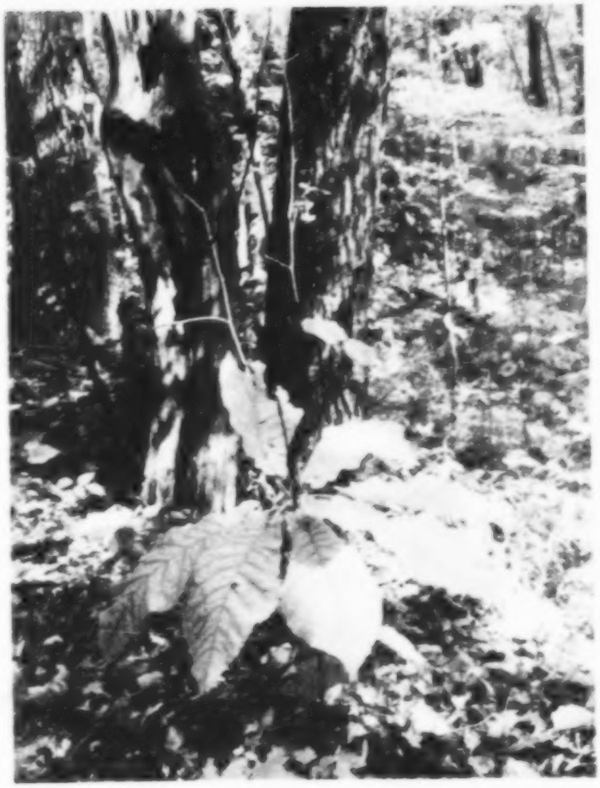

Figure 2—Magnolia fraseri *seedlings growing under a closed mesic cove-hardwood canopy at an elevation of 945 m (3,100 ft) in the southern Appalachians. The whorl of large, eared leaves is characteristic of the species.*

Foliage begins expanding the last week in April. Radial growth initiates in middle to late May and continues until the second week of August; at times it may last until the first week of September (*14*). Seedling reproduction is regarded as slow growing over most of its range when it is under closed or even partial canopies; however, Fraser magnolia seedlings even in clearcuts quickly fall behind other fast-growing intolerant species such as yellow-poplar, black cherry, and sweet birch.

Vegetative Reproduction—Although Fraser magnolia seedlings have difficulty in surviving to even an intermediate canopy position, stump sprouts survive more easily. It is highly possible that many, if not most, of the larger Fraser magnolia trees in the Appalachian forest region are of stump sprout origin; possibly many are seedling sprouts *(7)*. In this growth habit, the species closely resembles yellow-poplar and northern red oak. Seemingly, clearcutting with resultant sprout growth is the best way of reproducing Fraser magnolia.

Sapling and Pole Stages to Maturity

Growth and Yield—On most mesic sites, where Fraser magnolia does best, its sprouts grow vigorously from sapling to pole stage. In a Blue Ridge gorge, it was the last tree to begin growth in spring 1965 and 1966, but it grew very rapidly until growth cessation in late August *(14)*. Peak growth occurred at or below midslope. Average circumferential 3-year growth measured by band dendrometer at d.b.h. was 1.08 cm (0.424 in). On the flat, moist bottom land between slopes, Fraser magnolia trees were even-aged, about 50 years old, and formed part of a closed canopy.

In an intensive cleaning study established in spring 1960 in an 11-year-old mixed hardwood sapling stand near the Pink Beds on Pisgah National Forest, NC *(5)*, 14-year diameter growth of the four largest trees on one 0.01-ha (0.025-acre) plot was measured. Site quality was 28.7 m (94 ft) for yellow-poplar; there were 2,076 trees per hectare (840/acre) and 3.44 m²/ha (15 ft²/acre) of basal area after cleaning. Results were as follows:

Species	Diameter at age (yr) 11	14	17	21	25
	cm	*cm*	*cm*	*cm*	*cm*
Fraser magnolia	9.1	13.7	17.0	19.6	22.1
Yellow-poplar	5.8	10.9	14.7	20.6	26.7
Northern red oak	6.9	10.4	12.4	16.3	17.8
Sweet birch	4.1	7.1	10.2	14.0	15.5
	in	*in*	*in*	*in*	*in*
Fraser magnolia	3.6	5.4	6.7	7.7	8.7
Yellow-poplar	2.3	4.3	5.8	8.1	10.5
Northern red oak	2.7	4.1	4.9	6.4	7.0
Sweet birch	1.6	2.8	4.0	5.5	6.1

The 14-year increase in diameter for Fraser magnolia was 13.0 cm (5.1 in); for yellow-poplar, 20.8 cm (8.2 in); for northern red oak, 10.9 cm (4.3 in); and for sweet birch, 11.4 cm (4.5 in) *(19)*. Although at age 11 Fraser magnolia was larger than yellow-poplar by 3.3 cm (1.3 in), by age 21 yellow-poplar had exceeded it in size and was 4.6 cm (1.8 in) larger at age 25. At that time the plot contained 22.96 m²/ha (100 ft²/acre) of basal area and the stand was reduced to 1,483 trees/ha (600 trees/acre). This example serves to illustrate that Fraser magnolia sprout growth can be rapid in the early years of an even-aged stand. By maturity, however, Fraser magnolia is an intermediate tree in relation to the stand canopy. In this regard, growth of Fraser magnolia resembles that of Carolina basswood and cucumbertree; all three generally grow slower than yellow-poplar.

Fraser magnolia needs sunlight for growth and survival. This is shown by its generally contorted bole and branches, which result from growing leaders constantly twisting to exploit light from small openings. Occasionally a forest-grown Fraser magnolia can become as large as 61 cm (24 in) d.b.h. and 24 m (80 ft) tall *(7)*. The largest tree on record, growing in Philadelphia, PA, has a d.b.h. of 81 cm (32 in), a total height of 20 m (65 ft), and a crown spread of 15 m (50 ft).

No Fraser magnolia grows in the mountain counties of Virginia northeast of Roanoke Gap. The greatest volume is found in western Virginia, followed by North Carolina. Lesser volumes are found in West Virginia, Kentucky, and Tennessee, but specific data are not available *(11)*.

Stand and stocking data for Fraser magnolia in the Southeastern States are shown in table 1. Pulpwood-size trees through the 25.4 cm (10 in) diameter class account for 81 percent of the cubic-foot volume and 91 percent of the trees. The largest trees fall only into the 40.6 cm (16 in) diameter class and constitute less than 1 percent of all trees but 19 percent of total board-foot volume. Yields per acre are unavailable because of the sporadic occurrence and low density of Fraser magnolia.

Rooting Habit—Fraser magnolia seedlings have a deeply penetrating taproot. By the time seedlings become saplings, lateral roots are well developed *(7)*. Because of generally loose, friable soils, the root configuration of the trees remains unchanged through maturity except that roots grow larger.

Reaction to Competition—Fraser magnolia responds best to some form of even-age management. It is classed as being intermediate in tolerance to shade. Clearcutting is one way to regenerate it. At best, however, Fraser magnolia is likely to constitute less than 10 percent of any stand *(3,8)*. Since most of the regeneration is of sprout origin *(7,14)* it is highly dependent on the availability and distribution of Fraser magnolia trees in the original stand. Any additional trees that develop are likely to be seedling sprouts from damaged prelogging seedlings. Since

Table 1—Inventory of *Magnolia fraseri* combined for Virginia, North Carolina, South Carolina, and Georgia *(11)*

D.b.h. class	Number of trees	Merchantable stem volume in thousands		Saw log volume in thousands	
	thousands	*m³*	*ft³*	*m³*	*fbm*[1]
15 cm or 6 in	2,004	129.2	4,566	—	—
20 cm or 8 in	1,771	319.2	11,279	—	—
25 cm or 10 in	763	235.7	8,328	—	—
30 cm or 12 in	206	88.9	3,143	33.0	5,782
36 cm or 14 in	102	53.5	1,889	37.9	6,649
41 cm or 16 in	21	16.4	579	17.0	2,983
Total	4,867	842.9	29,784	87.9	15,414

[1] International ¼-inch log rule

many seedlings are found in mature stands, a one- or two-cut shelterwood would help seedlings grow to sapling size before the final harvest cut, and in this way they would have a competitive advantage over faster growing, more intolerant species. Because Fraser magnolia grows in clumps, early release by precommercial thinning to one stem accelerates its diameter growth and improves its form. Although Fraser magnolia can compete well on most sites with associated tree species for the first 40 or 50 years, at best it is short-lived and is prone to drop out of stands when it is 60 to 70 years old. When intermediate thinnings are part of stand management, as opposed to custodial management, Fraser magnolia is very often one of the first trees to be cut because of its generally poor form and susceptibility to damage. There is little incentive to manage it in the hope of producing high-quality timber.

Damaging Agents—Because of its thin bark, Fraser magnolia is very susceptible to fire and to logging damage *(7)*; both can lead to various wood rots.

Nectria magnoliae causes cankers on small or suppressed Fraser magnolia trees *(10)*. Whenever such trees become dominant or crown free, the cankers often heal. Fungi capable of causing rot of the central cylinder or in wounds are *Ganoderma applanatum, Fomes geotropus, Daedalea ambigua, Polyporus calkinsii, P. curtisii,* and *Laetiporus sulphureus.* White heartrot in living trees is caused by *Fomes sclerodermeus.* Sprout leaves may be heavily attacked by common powdery mildew, *Phyllactinia guttata. Phyllosticta magnoliae* causes a large black leaf spot. *Phoma pedunculi* and *Cytospora tumulosa* occur on branches. Fraser magnolia probably cannot withstand prolonged inundation, as evidenced by the cool, moist, but well-drained sites where it generally grows.

Several insect species can damage, if not kill, Fraser magnolia. *Euzophera ostricolorella* attacks the base of mature trees and *E. magnolialis* kills seedlings *(1)*. The ambrosia beetle, *Platypus compositus,* makes tunnels and larval cradles in the wood. *Xyloterinus politus* breeds in injured, dying, and recently cut trees, severely degrading lumber of infested wood because of adult tunneling. Larvae of the June beetle, *Phyllophaga forsteri,* feed on roots, and adults feed on foliage. Magnolia scale, *Neolecanium cornuparvum* feeds on current-year twig growth, seriously weakening and sometimes killing host trees.

Special Uses

In the lumber trade, Fraser magnolia is included with yellow-poplar sawtimber and pulpwood *(7)*. It has little value as firewood and generally has little value as sawtimber because of sweep and crook. Wildlife use larger defective trees of Fraser magnolia as den trees. Sprouts are browsed. In a mountainous area of western North Carolina, where Fraser magnolia sprouts occurred with a frequency of 20 percent and a density of 717 stems per hectare (290/acre), the species was 37-percent utilized by white-tailed deer *(5)*.

Frequent use is made of Fraser magnolia as an ornamental *(16)*.

Genetics

Certain distribution patterns are affected by polyploidy. Among magnolias, the relatively sharply peaked and restricted diploids, Fraser magnolia and umbrella magnolia, may be compared with the tetraploid cucumbertree *(21)*. Supposedly, a diploid species with extensive ecotypic variation should have a wider range than a polyploid derived from it; however, cucumbertree has the widest range of all three species.

No races or hybrids of Fraser magnolia have been reported, but a variety, *Magnolia fraseri* var. *pyramidata* (Bartr.) Pampanini, is occasionally mentioned *(13)*.

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Magnolia grandiflora L. Southern Magnolia

Magnoliaceae Magnolia family

Kenneth W. Outcalt

Southern magnolia (*Magnolia grandiflora*), also called evergreen magnolia, bull-bay, big-laurel, or large-flower magnolia, has large fragrant white flowers and evergreen leaves that make it one of the most splendid of forest trees and a very popular ornamental that has been planted around the world. This moderately fast-growing medium-sized tree grows best on rich, moist, well-drained soils of the bottoms and low uplands of the Coastal Plains of Southeastern United States. It grows with other hardwoods and is marketed as magnolia lumber along with other magnolia species to make furniture, pallets, and veneer. Wildlife eat the seeds, and florists prize the leathery foliage.

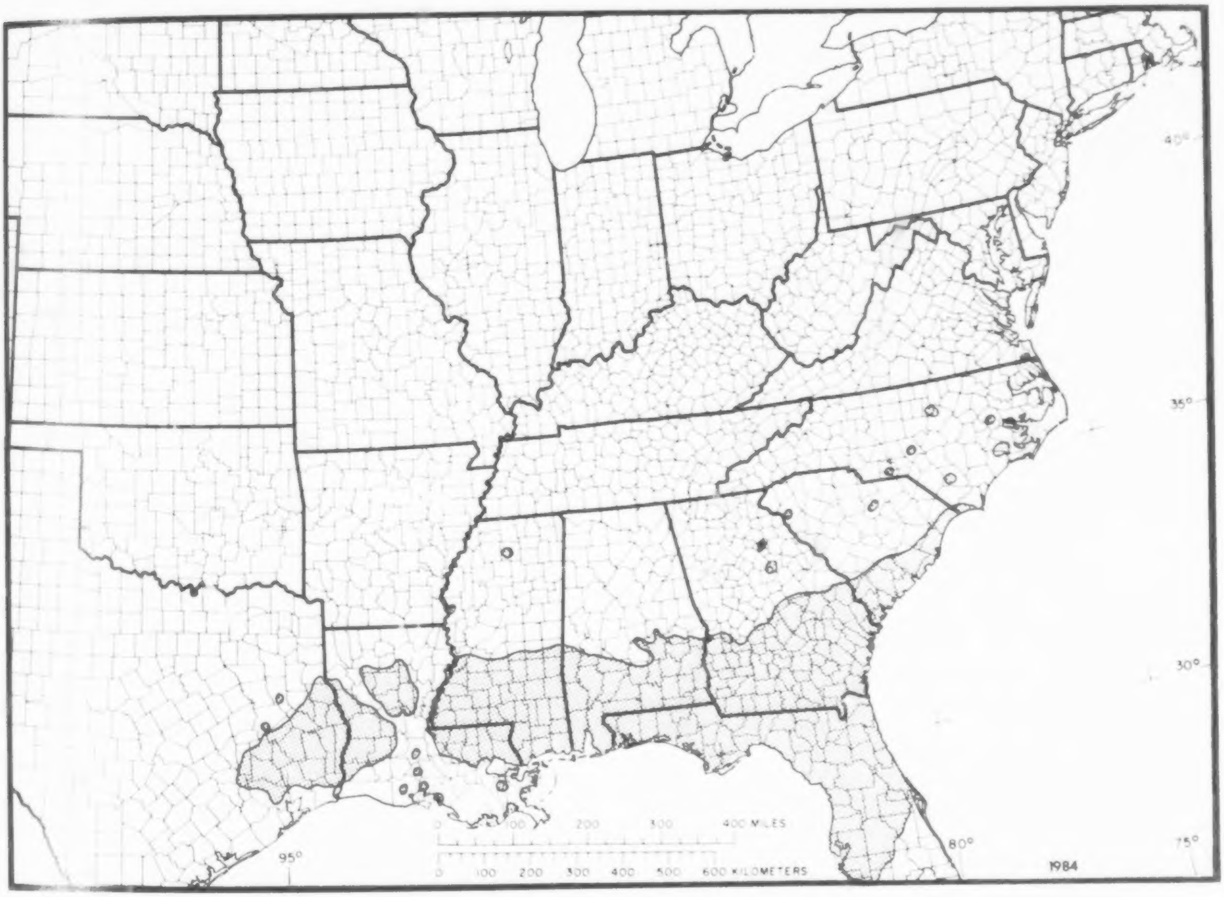

Figure 1—*The native range of southern magnolia.*

The author is Research Forester, Southeastern Forest Experiment Station, Asheville, NC.

Habitat

Native Range

The range of southern magnolia (fig.1) extends from eastern North Carolina, south along the Atlantic Coast to the Peace River in central Florida, then westward through roughly the southern half of Georgia, Alabama, and Mississippi, and across Louisiana into southeast Texas. It is most prevalent in Louisiana, Mississippi, and Texas *(12,14)*.

Climate

Southern magnolia grows in warm temperate to semitropical climates *(2)*. The frost-free period is at least 210 days and is more than 240 days for much of the range. Average January temperatures along the coast are 9° to 12° C (49° to 54° F) in South Carolina and Georgia and 11° to 21° C (52° to 70° F) in Florida. Coastal temperatures average 27° C (80° F) during July. Temperatures below -9° C (15° F) or above 38° C (100° F) are rare within the species natural range.

Annual rainfall averages 1020 to 1270 mm (40 to 50 in) in the northeastern portion of the range and 1270 to 1520 mm (50 to 60 in) in other areas. A small area along the Gulf Coast receives 1520 to 2030 mm (60 to 80 in) yearly. In the Atlantic Coastal Plain, summer is usually wettest and autumn driest. Periodic summer droughts occur in the western part of the range.

Soils and Topography

Southern magnolia grows best on rich, loamy, moist soils along streams and near swamps in the Coastal Plain *(2,14)*. It also grows on mesic upland sites where fire is rare. Although primarily a bottomland species it cannot withstand prolonged inundation. Thus, it does not appear in the first bottoms but grows mostly on the oldest alluvium and outwash sites.

Southern magnolia is found on a number of different soils including those in the orders Spodosols, Alfisols, Vertisols, and Ultisols. Along the coast it grows primarily on soils of the Leon, Bladen, Coxville, Portsmouth, Lake Charles, and Crowley series. Farther inland in central Florida, Georgia, and States to the west, it is found on the Norfolk, Ruston, Greenville, Memphis, Grenada, Caddo, and Beauregard soils.

No part of its natural range is higher than 150 m (500 ft) in elevation and most of it is less than 60 m (200 ft). Coastal areas within its range are all less than 30 m (100 ft) above sea level. In the northern parts of the range in Georgia and Mississippi, it is found at elevations of 90 to 120 m (300 to 400 ft).

Associated Forest Cover

Southern magnolia rarely forms pure stands but is usually associated with a variety of mesic hardwoods. It is a minor component of the following forest cover types *(7)*: Southern Redcedar (Society of American Foresters Type 73), Cabbage Palmetto (Type 74), Loblolly Pine–Hardwood (Type 82), Live Oak (Type 89), Swamp Chestnut Oak–Cherrybark Oak (Type 91), and Sweetbay–Swamp Tupelo–Redbay (Type 104). Other trees commonly associated with southern magnolia are beech *(Fagus grandifolia)*, sweetgum *(Liquidambar styraciflua)*, yellow-poplar *(Liriodendron tulipifera)*, southern red oak *(Quercus falcata)*, white oak *(Q. alba)*, mockernut hickory *(Carya tomentosa)*, and pignut hickory *(C. glabra)*.

Understory associates include a wide variety of species. Typical examples are devils-walkingstick *(Aralia spinosa)*, flowering dogwood *(Cornus florida)*, swamp dogwood *(C. stricta)*, beautyberry *(Callicarpa americana)*, strawberry-bush *(Euonymus americanus)*, southern bayberry *(Myrica cerifera)*, Virginia creeper *(Parthenocissus quinquefolia)*, poison-ivy *(Toxicodendron radicans)*, sweetleaf *(Symplocos tinctoria)*, greenbriers *(Similax* spp.), and muscadine grape *(Vitis rotundifolia)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The large, white, fragrant flowers are perfect *(19)* and appear from April to June. The fleshy conelike fruit matures from September through the late fall. When the fruit matures and opens, seeds 6 to 13 mm (0.25 to 0.5 in) long emerge and hang temporarily suspended by slender, silken threads before dropping *(2)*.

Seed Production and Dissemination—The seeds are drupelike, with a soft, fleshy outer seedcoat and an inner stony portion. Southern magnolia is a prolific seed producer and good seed crops normally occur every year *(14)*. Trees as young as 10 years old can produce seed, but optimum seed production under forest conditions usually does not occur until age 25. Cleaned seeds range in number from 12,800 to 15,000/kg (5,800 to 6,800/lb) and average 14,200/kg (6,450/lb) *(19)*. Seed viability averages about 50 percent. The relatively heavy seeds are disseminated mostly by birds and mammals, but some may be spread by heavy rains.

Seedling Development—Seeds usually germinate the first or second spring following seedfall. Germination is epigeal *(19)*. The best natural seedbed is a rich, moist soil protected by litter. Even though viable, seeds rarely germinate under the parent tree because of reported inhibitory effects *(3)*.

Seedlings are very susceptible to frost damage, and even a slight freeze can cause mortality. Partial shade is beneficial for the first 2 years of seedling growth. Under favorable conditions growth is quite rapid. In nurseries, seedlings usually grow 46 to 61 cm (18 to 24 in) the first year *(2)*.

Vegetative Reproduction—Mature southern magnolia commonly develops root and stump sprouts *(3)*. Portions of lower limbs of saplings often become imbedded in the forest floor where they develop roots, eventually producing separate trees. Air-layering, stem cuttings, and grafts have all been used to propagate the species for ornamental plantings.

Sapling and Pole Stages to Maturity

Growth and Yield—On good sites, southern magnolia trees (fig. 2) average 18 to 24 m (60 to 80 ft) tall and 61 to 91 cm (24 to 36 in) in d.b.h. in 80 to 120 years. Heights of 30 to 38 m (100 to 125 ft) have been reported in Florida *(2)*. Annual diameter growth for large mature trees in an east Texas stand was .24 cm (.09 in) *(8)*. In unmanaged natural stands in the Florida panhandle, trees without overtopping competition will average .76 cm (.3 in) of diameter growth and 0.46 m (1.5 ft) of height growth per year through age 50. Under natural conditions, many trees spend 10 to 20 years in the understory before they reach the upper canopy. Annual diameter growth for these trees is .51 cm (.2 in) and average height growth is .31 m (1.0 ft) to age 50 years.

Rooting Habit—Southern Magnolia is a deep-rooted species, except on sites with a high water table. Seedlings quickly develop one major taproot. As trees grow the root structure changes. Trees of sapling stage and beyond have a rather extensive heart root system (i.e. several to many sunken roots grow down from the root collar of the tree trunk). Older trees may develop a fluted base with the ridges corresponding to the attachment of major lateral roots.

Reaction to Competition—Overall, southern magnolia is tolerant of shade. It can endure considerable shade in early life *(8)*, but needs more light as it becomes older *(2)*. It will invade existing stands and is able to reproduce under a closed canopy *(3,8)*. Once established, it can maintain or increase its presence in stands by sprout and seedling production that grows up through openings, which occur sporadically in the canopy.

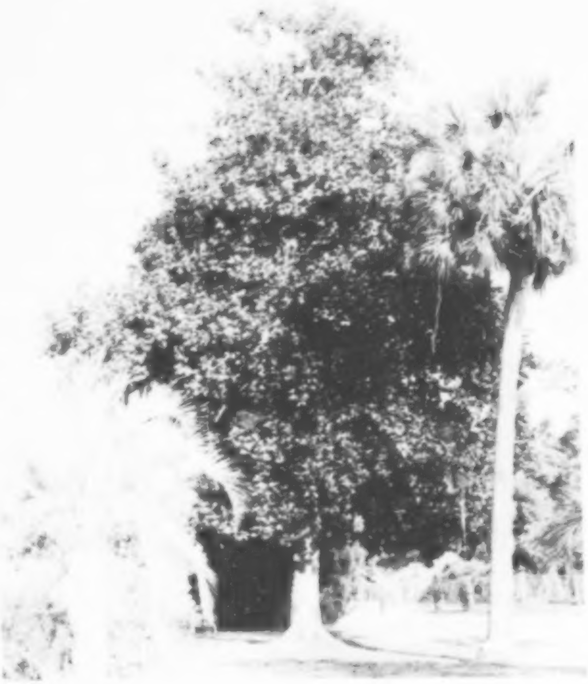

Figure 2—*Southern magnolia grown as an ornamental in Florida.*

Southern magnolia is considered to be one of the major species of the potential climax forest of the southeastern Coastal Plains *(3,6,15,16,20)*. In the past, regular burning restricted the species to the wetter sites, as seedlings are easily killed by fire. Older trees, however, due to bark characteristics, are quite fire resistant *(3,10)* and even if the tops are killed, they sprout vigorously. Since the advent of improved fire control, southern magnolia has been migrating onto mesic upland sites and establishing itself, along with associated hardwoods, as part of the climax forest.

Damaging Agents—Young southern magnolia are susceptible to fire-caused injury and mortality. Winter droughts can cause extensive dieback and mortality. A number of fungi, including species of *Cladosporium*, *Colletotrichum*, *Glomerella*, *Phyllosticta*, and *Septoria* cause leaf spots but these seldom result in any significant damage *(2)*. A leaf spot caused by *Mycosphaerella milleri* can be a problem on nursery seedlings. A number of *Fomes* and *Polyporus* fungi can cause heartrot in southern magnolia. Heavy infestations of magnolia scale *(Neolecanium cornuparvum)* can kill branches or entire trees *(18)*. Oleander pit scale *(Asterolecanium pustulans)* and tuliptree scale *(Toumeyella liriodendri)* attack and injure southern magnolia, but rarely cause mortality *(1)*. A variety of other pests, including tuliptree aphid *(Illinoia liriodendri)*, striped mealybug *(Ferrisia virgata)*, leaf weevil *(Odontopus calceatus)*, magnolia leafminer *(Phyllocnistis magnoliella)*, and spider mite *(Tetranychus magnoliae)* feed on this species *(18)*. *Euzophera magnolialis*, a wood borer, can injure or kill nursery seedlings.

Special Uses

Because of its showy flowers and lustrous evergreen foliage, southern magnolia is a valuable and extensively planted ornamental. In many urban areas where other species do poorly, this magnolia can grow because of its resistance to damage by sulfur dioxide. The seeds are eaten by squirrels, opossums, quail, and turkey *(9)*. The leaves, fruits, bark, and wood yield a variety of extracts with potential applications as pharmaceuticals *(4,5)*.

Genetics

No work has been done to characterize individual populations. Extensive breeding has been done to develop races of southern magnolia for ornamental use *(13)*. Common varieties include *Magnolia grandiflora lanceolata* with a narrow pyramidal habit and *M. grandiflora gallissoniensis*, reported to be cold hardy *(17)*.

Southern magnolia has been hybridized with sweetbay *(Magnolia virginiana)* and *M. guatemalensis*.

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Magnolia virginiana L. Sweetbay

Magnoliaceae Magnolia family

David S. Priester

Sweetbay (*Magnolia virginiana*), also called swamp-bay, white-bay, laurel, swamp, or sweet magnolia, and swamp-laurel, is at times confused with loblolly-bay (*Gordonia lasianthus*) and redbay (*Persea borbonia*), since "bay" is the term commonly used in referring to any of these three species. Sweetbay is readily distinguished from the others by the white pubescence of its lower leaf surfaces (*11,21*). Sweetbay is a slow-growing small to medium-sized tree found on wet, often acid soils of coastal swamps and low lands of the Coastal Plains. The soft aromatic straight-grained wood is easily worked and finishes well, so it is much used for veneer, boxes, and containers. Its flowers and foliage make it an attractive landscape tree.

Habitat

Native Range

The range of sweetbay (figs. 1, 2) extends chiefly along the Atlantic and Gulf Coastal Plains from Long Island south through New Jersey and southeastern Pennsylvania to southern Florida; west to eastern Texas, and north into southern Arkansas and southwest Tennessee; sweetbay also appears in isolated portions of eastern Massachusetts, where it may reflect only older ornamental plantings. Sweetbay is most abundant in the States of Alabama, Georgia, Florida, and South Carolina (*13*).

Climate

Rainfall per year within the geographic range of sweet bay varies from a minimum of 1220 mm (48 in) in the northern reaches of the Atlantic Coastal Plain to a maximum of 1630 mm (64 in) in some areas of the southern Gulf Coastal Plain and south Florida (*13*).

Because of the extensive geographic range of sweetbay, the average length of the growing season extends from approximately 180 days near the northern limit of the range to about 340 days in the south. The climate is described as humid to moist subhumid with an average minimum temperature range of -23° C (-10° F) in Massachusetts to 4° C (40° F) in southern Florida (*13*).

Soils and Topography

In the Atlantic and Gulf Coastal Plain, sweetbay is found mainly east of the Mississippi River on sites that are usually moist throughout the year. Sweetbay sites are characterized by acid soils of low base saturation and with poor to very poor drainage and are frequently flooded during the winter or wet seasons. Trees are not usually found in bottoms of major rivers (*4*). Many sweetbay sites have never been cultivated and represent virgin soils. These soils are the poorly drained Ultisols, the ground water Spodosols, and Coastal Plain Histosols. Typical soils where the species is found are Bayboro and Portsmouth in South Carolina (*24,25*) and Bibb and Myatt soils in Alabama (*4*).

Most of the natural range of sweetbay is less than 61 m (200 ft) above sea level, although some isolated populations exist at higher elevations. The latitudinal range of sweet bay is approximately 26° N. to 41° N. (*13*).

Associated Forest Cover

Sweetbay is a major species in only one forest cover type, Sweetbay-Swamp Tupelo-Redbay (Society of American Foresters Type 104) (*3*). Also associated with this type are such hardwoods as red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), loblolly-bay, redbay, sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), laurel oak (*Q. laurifolia*), yellow-poplar (*Liriodendron tulipifera*), American holly (*Ilex opaca*), Carolina ash (*Fraxinus caroliniana*), southern magnolia (*Magnolia grandiflora*), and flowering dogwood (*Cornus florida*); conifers such as slash pine (*Pinus elliottii*), pond pine (*P. serotina*), longleaf pine (*P. palustris*), loblolly pine (*P. taeda*), Atlantic white-cedar (*Chamaecyparis thyoides*), baldcypress (*Taxodium distichum*), and pondcypress (*T. distichum* var. *nutans*). Varying soil and moisture conditions influence the composition of this type. Sweetbay can be totally eliminated in this type by deep flooding of swamp and pond centers (*15*).

Undergrowth of sweetbay sites is as diverse as are the soils. Some of the evergreen shrubs and small trees are buckwheat-tree (*Cliftonia monophylla*), swamp cyrilla (*Cyrilla racemiflora*), southern bayberry (*Myrica cerifera*), odorless bayberry (*M. inodora*), dahoon (*Ilex cassine*), yaupon (*I. vomitoria*), large gallberry (*I. coriacea*), inkberry (*I. glabra*), coast

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The author was Biologist (now deceased), formerly with the Southeastern Forest Experiment Station, Asheville, NC.

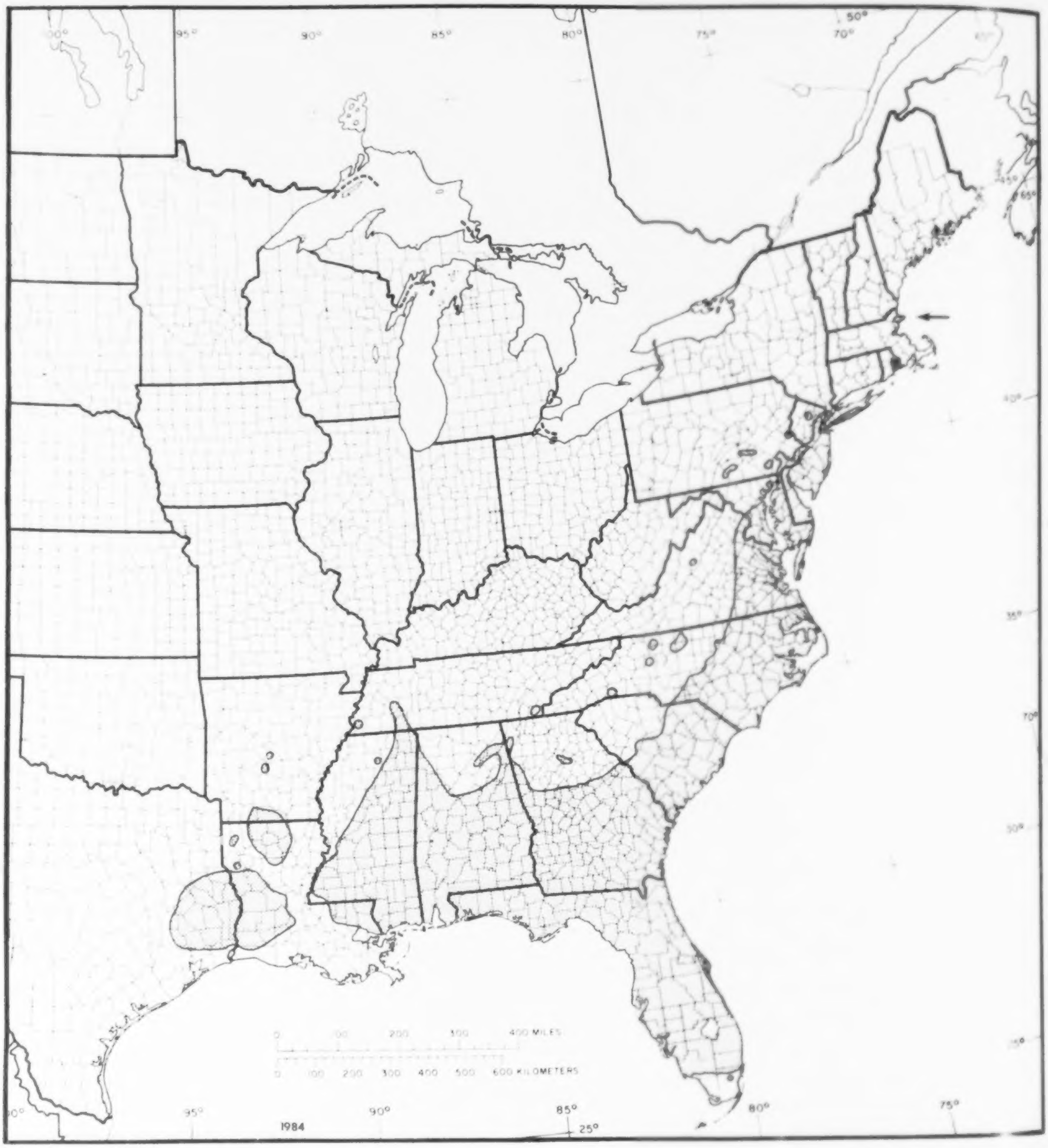
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Figure 1—*The native range of sweetbay.*

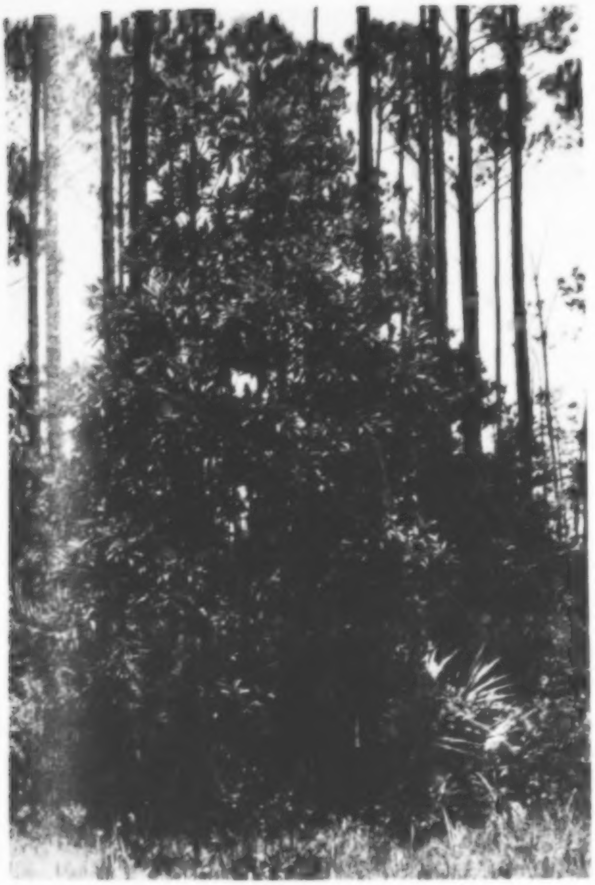

Figure 2—*Sweetbay.*

leucothoe (*Leucothoe axillaris*), fetterbush lyonia (*Lyonia lucida*), staggerbush lyonia (*L. mariana*), sweet pepperbush (*Clethra alnifolia*), and small switchcane (*Arundinaria tecta*). The deciduous shrubs commonly found are Virginia-willow (*Itea virginica*), hazel alder (*Alnus serrulata*), swamp dogwood (*Cornus stricta*), red chokecherry (*Sorbus arbutifolia*), poison-sumac (*Toxicodendron vernix*), American snowbell (*Styrax americanus*), and possumhaw viburnum (*Viburnum nudum*) (*3*).

Such perennial vines as greenbriers (*Smilax* spp.), muscadine grape (*Vitis rotundifolia*), poison-ivy (*Toxicodendron radicans*), Virginia creeper (*Parthenocissus quinquefolia*), southeast decumaria (*Decumaria barbara*), and climbing hempweed (*Mikania scandens*) may also occur. Some common herbaceous species present are ferns (*Polypodium* spp.), mosses (*Polytrichum* spp.), pitcher plants (*Sarracenia* spp.), pipeworts (*Eriocaulon* spp.), yellow-eyed grasses (*Xyris* spp.), and sedges (*Cyperus* spp.) (*3*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—The perfect flowers of sweetbay are fragrant; they are 5 to 7.5 cm (2 to 3 in) in diameter and 5 cm (2 in) deep. Three pale sepals surround six to nine creamy white petals. Inside the cup-shaped corolla are many stamens with purple bases, and within these stamens are many pistils spirally inserted on a spikelike receptacle (*6,9*). The flowers are borne singly at the ends of branches and continue to open during a period of several weeks from April into July. Pollination is by insects (*20,23*).

The fruit is an ellipsoid or subglobose aggregate 2.5 to 5 cm (1 to 2 in) long and 1.25 to 3 cm (0.5 to 1.25 in) in diameter and consists of many one- or two-seeded follicles (*15,20*). The fruits become ripe from July into October and are dull red, brownish red, or nearly green at maturity (*2,20*). At maturity, the follicles dehisce, and the 6 to 13 mm (0.25 to 0.5 in) long scarlet seeds emerge to hang suspended for a time by fine silky threads (*15*).

Seed Production and Dissemination—Sweetbays usually produce some fruit annually, but the yields are small (*11*). Seed dispersal is by wind, birds, and occasionally by water and occurs soon after ripening (*23*).

The seed of sweetbay is drupelike. The outer portion of the outer seedcoat is fleshy, oily and soft; the inner portion is stony. If seeds are to be sown soon after collection, the fleshy outer portion should be removed by maceration in water or by rubbing on hardware cloth. Cleaned seeds average about 16,600/kg (7,530/lb) (*23*).

Seeds can be kept either cleaned or in the dried pulp for several years with little loss of viability if they are stored in sealed containers at 0° to 5° C (32° to 41° F). Seeds stored at higher temperatures should not be cleaned (*23*).

Seedling Development—Sweetbay seeds show embryo dormancy that can be overcome by 3 to 6 months of low temperature stratification at 0° to 5° C (32° to 41° F). Various tests with stratified seeds have yielded germinative capacities averaging from 32 to 50 percent. Germination is epigeal *(23)*.

In the nursery, unstratified seeds may be sown in the fall or stratified seeds may be sown in late winter or spring. Spring sowing appears to be best in areas where depredation by rodents is a serious problem. The sown seeds should be covered with about 6 mm (0.25 in) of soil, and mulch should be kept on the beds until all danger from frost is past. The emerged seedlings need half shade during much of their first summer. Normally, plantings are established with 1-0 seedlings *(23)*.

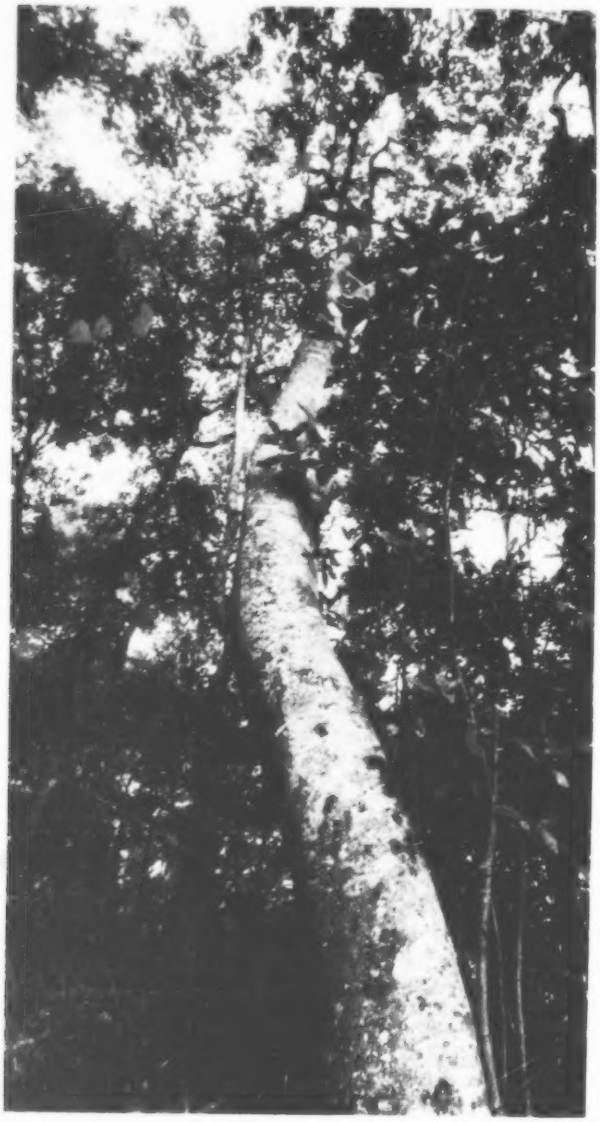

Figure 3—*Sweetbay with root-collar sprouts resulting from wildfire wound.*

The possibilities for natural regeneration of sweetbay are greatest in natural openings or in clearcut swamps. In such openings, survival of the germinated seedlings is high unless they are inundated for an extended period. First-year growth usually averages between 30 and 60 cm (12 to 24 in). First-year seedlings are fairly tolerant of shade and competing vegetation *(19)*.

Vegetative Reproduction—Sweetbay can be propagated through layering and grafting and through cuttings treated with root-promoting chemicals *(7)*. Sweetbay stumps produce sprouts (fig. 3) but their vitality and growth potential are not known *(18)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Sweetbay is usually smaller in diameter than the southern magnolia *(15)*. The trunk of the tree is usually straight with small, short branches forming a narrow round-topped head and branchlets which become glabrous in their second year. Growth rate averages poor to medium *(19)*, though it can be rapid for the first few years under favorable conditions. As a shrub, growth and form are diverse and irregular.

In the more northern climates sweetbay is mainly a shrub, but it is a tree in the southern portions of the range. As a shrub, sweetbay usually attains a height between 60 and 150 cm (24 and 60 in). In the southern portions of the range the tree may range in height from approximately 15 to 30 m (50 to 100 ft) and vary in d.b.h. from less than 10 to 90 cm (4 to 36 in). A record-size sweetbay 128 cm (50 in) in d.b.h. and 27.7 m (91 ft) tall has been recorded in Florida *(1,15)*.

Rooting Habit—No information is available on rooting habits of sweetbay.

Reaction to Competition—Sweetbay is classed as intermediate in tolerance to shade and to flooding as evidenced by its growth in bay heads and mixed swamps that are only seasonally shallow-flooded *(16)*, and at the outer edges of cypress ponds that are only seasonally flooded *(17)*. Among southern hardwoods, sweetbay is very resistant to fire; and as bark thickness increases, so does this resistance *(5)*. Repeated burning, however, may eliminate sweetbay from some of the poorly drained flatwoods and Carolina bays *(22)*.

Damaging Agents—Fungal infection of sweetbay leaves is a common occurrence. Small angular spots may be found in early summer and are caused by the *Cercospora* stage of *Mycosphaerella milleri*. The ascospore stage of *M. milleri* may be found on overwintered, fallen leaves. *M. glauca*, which causes large circular leaf spots, can be found any time of the year on attached leaves. *Sclerotinia gracilipes*, a species confined to sweetbay, can cause the petals of the flower to rot.

A light-brown stain in the wood is caused by *Cephalosporium pallidum* and is associated with the galleries of an ambrosia beetle *(Xyleborus affinis)*. Ambrosia beetles usually attack sick or dying trees *(8,10)*.

Special Uses

Its persistent leaves, fragrant white flowers, and decorative fruit make sweetbay attractive as an ornamental shrub or tree *(11)*. Larger trees are used for veneer and some box lumber. The tree is also utilized to some degree as pulpwood *(15)*.

Sweetbay is also a favorite food of deer and cattle. Deer browse the leaves and twigs all year. Cattle utilize sweetbay especially in the winter, when it can account for as much as 25 percent of their winter diet. Analysis of browse samples from Georgia and east Texas indicate that sweetbay contains 10 percent crude protein. The seeds are a favorite food of gray squirrels and are eaten to a lesser extent by white-footed mice, wild turkey, quail, and songbirds *(11,12,15)*.

Genetics

As previously stated, sweetbay in the northern portions of its range is basically a shrub and becomes more treelike in the southern portions of its range. There is no information readily available on race differences of sweetbay.

A hybrid cultivar, *Magnolia × thompsoniana*, which is intermediate in character between *M. virginiana* and *M. tripetala*, is grown as a garden plant in the Eastern United States and in Europe. It was first raised in an English nursery more than 200 years ago *(21)*. No varieties of sweetbay are recognized *(14)*.

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Manilkara bidentata (A. DC.) Chev. **Ausubo, Balata**

Sapotaceae **Sapodilla family**

P. L. Weaver

Ausubo *(Manilkara bidentata)*, also known as balata, is a large evergreen forest tree that was probably the most important timber tree of Puerto Rico. It grows best in Puerto Rico on alluvial plains where it may reach the age of 400 years. Ausubo is extremely tolerant of shade. The strong and attractive wood makes it highly valued commercially and it is widely used in the tropics for many wood products. The tree is often tapped for its milky latex, the source of balata gum. Although growth is slow, ausubo is planted for shade and timber.

Habitat

Native Range

Ausubo is native to Puerto Rico, widely distributed throughout the West Indies, and ranges from Mexico through Panama to northern South America, including the Guianas and Venezuela, to Peru, and to northern Brazil *(9,22)*.

In Puerto Rico, ausubo is native to the moist coastal and limestone forests, and to lower mountain forests. Ausubo ranges from near sea level up to 600 m (2,000 ft) in elevation. The tree is a primary species and is very shade tolerant.

Climate

In Puerto Rico, ausubo is found in the Subtropical Moist, Subtropical Wet, and Subtropical Rain Forest life zones. Annual rainfall in these forests varies from 1500 to 4000 mm (59 to 157 in). Temperatures range from a mean minimum in January of 16° C (61° F) to a mean maximum of 31° C (88° F) in August *(8)*, the extremes for the range of ausubo on the island. Evapotranspiration over the same regions varies between 1400 and 1800 mm/yr (55 and 71 in/yr), with the lowest measurements in the mountainous interior.

Throughout the West Indies, ausubo grows in areas where the annual rainfall varies from 1500 to 4000 mm (59 to 157 in) (table 1). In South America, many areas probably receive more than that amount. In the Bajo Calima region of Colombia, west of the city of Cali, annual rainfall in Tropical Rain Forest approaches 7000 mm (276 in). All sites are frost free.

Soils and Topography

In Puerto Rico, ausubo is native to acid, clay soils, derived in situ, or deposited by alluvial or colluvial processes. Existing inventories indicate that it grows mainly on soils of the orders Inceptisol and Oxisol. Parent rocks include andesites and limestone. In Trinidad, ausubo thrives on a variety of soils ranging from clays through sands, including rocky soils, and on several different geologic formations *(27)*. Physiographically, it is found on slopes and flats, and in coves. In Trinidad it is common on hills, and in Puerto Rico, it attains its best development on alluvial plains. In Suriname, it is common along river banks *(31)*.

Associated Forest Cover

In Puerto Rico, ausubo is associated with tabonuco *(Dacryodes excelsa)*, guaraguao *(Guarea guidonia)*, granadillo *(Buchenavia capitata)*, and motillo *(Sloanea berteriana)* in the Subtropical Wet Forest classification according to Holdridge *(18)*. In the Luquillo Mountains of northeastern Puerto Rico, species assemblages produced by the use of statistical clustering techniques revealed that ausubo occurs on upper slopes along with granadillo *(13)*.

Elsewhere within its range, ausubo is a constituent of several different forest types (table 1), attaining its best development in Lowland Rain Forest, or Lower Montane Rain Forest (classification according to Beard) *(1,2,4,5)*.

Species associated are numerous and vary with locale *(4)*. In Trinidad, for example, ausubo is found in the Dry Evergreen Formation and Littoral Woodland along with royal palm *(Roystonea oleracea)*, sierra palm *(Prestoea montana)*, and timite *(Manicaria saccifera)*. It is also found in Evergreen Seasonal Forest in the *Carapa–Eschweilera* association and in the *Peltogyne* association. Finally, it is found scattered in the Lower Montane Rain Forest.

Life History

Reproduction and Early Growth

Mature ausubo (fig. 1) is characterized by a dense growth of horizontal branches with layered foliage and dark green elliptic, alternate leaves with many

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The author is Research Forester, Southern Forest Experiment Station, New Orleans, LA. (Research on this species was done in cooperation with the University of Puerto Rico, Rio Piedras.)

faint parallel veins. A white latex appears in droplets from cut leaves and incisions in the trunk and stems. Large trunks have broad rounded buttresses spreading at the base.

In Puerto Rico, the tree attains a height of 30 m (100 ft) and diameter of 1.3 m (4 ft) on the best sites. On favorable sites elsewhere within its range, the tree will grow 45 m (150 ft) in height and nearly 200 cm (79 in) in diameter.

Flowering and Fruiting—In Puerto Rico, the white perfect flowers are borne annually on a stalk at the beginning of the wet season, mainly from May through late August, with occasional late autumn flowering. Fruits develop through the autumn with the principal fruit drop in winter and early spring *(15)*. In Trinidad, ausubo flowers at the beginning of the dry season, January to February, and the fruit ripens by April and May *(27)*. In both regions, good flowering and fruiting is at intervals of 3 to 4 years.

At randomly placed collection stations comprised of 0.5 m^2 (5.4 ft^2) screen baskets in the Subtropical Wet Forest of Puerto Rico, ausubo dropped some 70 fruits in 39 months. Of the species of trees observed, ausubo ranked 16th in number of fruits collected *(15)*.

Seed Production and Dissemination—Ausubo fruits are globose berries about 2.5 cm (1 in) in diameter and usually contain a single, shiny, black seed, surrounded by a sweet, gummy pulp that is edible. Occasionally, two seeds per fruit are found *(21,27)*.

In unpublished experimental work conducted at the Institute of Tropical Forestry, 1,280 air-dried seeds per kilogram (580/lb) were counted. Cutting tests showed that 35 percent of the seeds were hollow. Moisture accounted for about 30 percent of the weight of the seeds.

Seed dispersal is limited to the vicinity of the parent tree unless animals consume or carry the fruits. Agouti and other animals eat the fruit in Trinidad *(27)*, while in Puerto Rico birds have been identified as dispersal agents.

Seedling Development—Germination is epigeous and irregular over a long period, with some seed germinating in the second year. Trials in Trinidad yielded only 10 percent germination, and efforts to improve it by soaking in water or slightly cracking the seed were a failure *(27)*. In Puerto Rico, 100 seeds per treatment were stored at room temperature and at 4° C (40° F) in paper sacks and sealed jars for periods of 1, 2, 3, and 6 months. A control was sown immediately. Germination for the treated seeds was essentially nil while the control showed 60 percent success. It was concluded that storage by the means tested was unsatisfactory.

Table 1—Presence of ausubo *(Manilkara bidentata)* in tropical forests of the Western Hemisphere

Country	Forest type classification[1]	Annual rainfall	
		mm	*in*
Puerto Rico *(16)*	Subtropical Moist Forest[1]	1000 to 2000	39 to 79
	Subtropical Wet Forest[1]	2000 to 4000	79 to 157
Dominica *(16)*	Lower Montane Rain Forest[2]	– 3000	– 118
	Secondary Rain Forests[2]	– 2000	– 79
St. Lucia *(4)*	Lowland Rain Forests[2]	2000 to 2500	79 to 98
	Lower Montane Rain Forest[2]	– 3000	– 118
	Secondary Woodlands[2]	2000 to 2500	79 to 98
Grenada *(4)*	Lowland Rain Forest[2]	2000 to 2500	79 to 98
	Lower Montane Rain Forest[2]	– 3000	– 118
	Dry Scrub Woodland[2]	– 1500	– 59
	Secondary Rain Forest[2]	2000 to 2500	79 to 98
Barbados *(4)*	Dry Scrub Woodland[2]	– 1500	– 59
British Virgin Islands *(4)*	Xerophytic Rain Forest[2]	– 1500	– 59
Trinidad *(3)*	Lower Montane Rain Forest[2]	2000 to 2500	79 to 98
Colombia *(19,32)*	Tropical Rain Forest[1]	– 7000	– 276
	Tropical Moist Forest[1]	2000 to 4000	79 to 157
British Guyana *(17)*	Evergreen Seasonal Forest[2]	1700 to 1900	67 to 75
Venezuela *(3)*	Lower Montane Rain Forest[2]	2000 to 3000	79 to 118
Suriname *(20,31)*	Rain Forest[3]	2000 to 2500	79 to 98
	Upland Rain Forest[3]	2000 to 2500	79 to 98

[1] Holdridge *(18)*—Puerto Rico

[2] Beard *(1, 2, 3, 4, 5)*—Dominica, St. Lucia, Grenada, Barbados, British Virgin Islands, Trinidad, Colombia, Guyana, and Venezuela

[3] Schulz *(31)*—Suriname

Seedlings in the wild are capable of growing under heavy shade and in herbaceous cover. Average height at the end of the first year is 12 cm (5 in), and after 5 years about 4.5 m (15 ft).

Artificial regeneration is best attained by direct sowing of fruits or transplanting of potted seedlings. Ausubo seeds should be sown in moist leaves because they are not capable of emerging from the soil *(26)*. "Limited success" has been achieved with bare root plantings after 1 year in the nursery, but if seedlings are left too long in the beds, the taproot proves to be a problem *(27)*.

In experimental work at the Institute of Tropical Forestry, seeds were sown in nursery beds in the sun and under shaded conditions. After 10 months, those in the sun were twice as tall as the shaded specimens. Direct out-planting of potted seedlings under heavy shade in the limestone forest on the north coast showed survival rates greater than 90 percent after 10 months. The seedlings, however, were sensitive to drought. Most had wilted and yellowed after a prolonged period without rain.

Vegetative Reproduction—Except when quite young, ausubo does not coppice, nor does it produce root suckers *(27)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth of ausubo is slow in the sapling stage and slow to intermediate in the pole stage through maturity. Height is about 0.3 m (1 ft) at 1 year, and about 4.5 m (15 ft) in 5 years. Annual diameter increment in an early secondary stand in St. Just (table 2), where the stems ranged from 4 to 13 cm (1.6 to 5.1 in) in diameter, averaged 0.58 cm (0.23 in) over a 2-year period.

On an understocked 0.4 ha (1 acre) plantation in Trinidad, after 21 years volume mean annual increment (MAI) averaged only 2.37 m^3/ha (33.86 ft^3/acre). Diameter and height MAI for plantations in both Trinidad and Puerto Rico show that the former varies from 0.51 to 0.81 cm (0.20 to 0.32 in), and the latter from 0.2 to 1.1 m (0.66 to 3.6 ft), depending on site (table 2). Measurements of annual diameter increments for 17 years in previously thinned Subtropical Wet Forest of the Luquillo Mountains shows an average annual growth of 0.51 to 0.58 cm (0.20 to 0.23 in).

Rooting Habit—By 2 years of age, the seedling has a taproot. When older, it has a strong, moderately deep root system making the species wind-firm *(27)*.

In the study of a single ausubo tree in the Luquillo Experimental Forest, a root-to-shoot-to-leaf ratio of

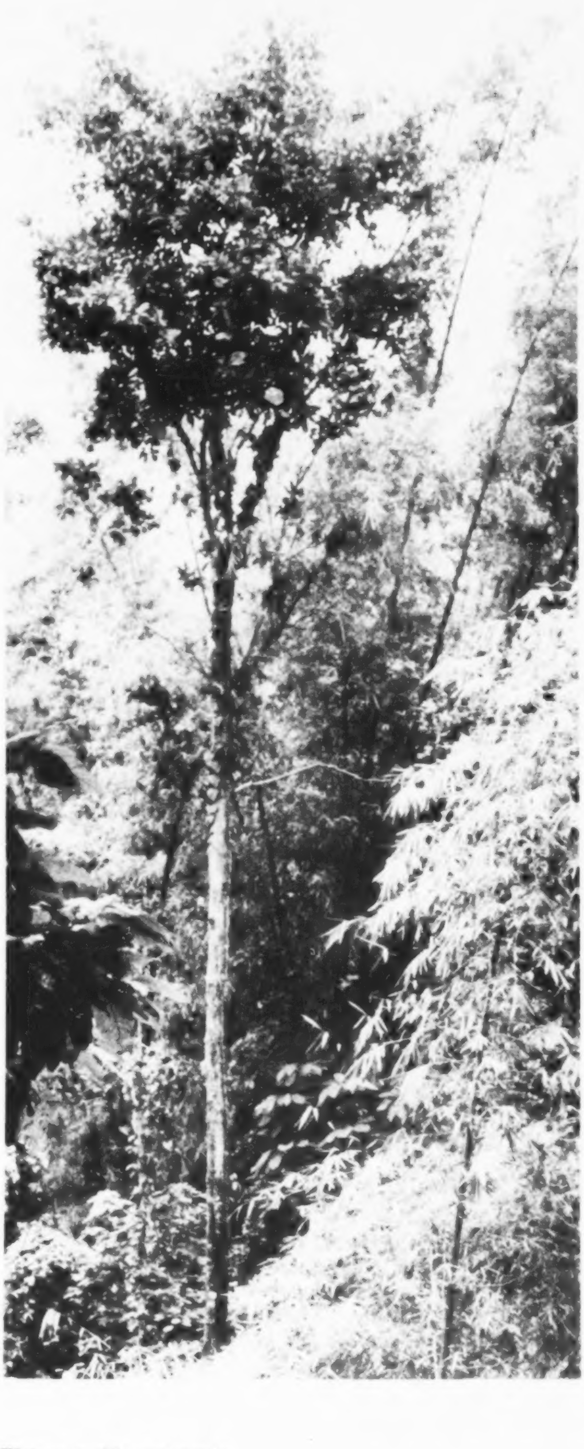

Figure 1—*Mature ausubo.*

Table 2—Annual increment for ausubo (*Manilkara bidentata*) in the Western Hemisphere

	Site characteristics			Stand		Annual increment			
Location	Elevation	Rainfall	Soil	Density[1]	Age	Height	D.b.h.	Basal area	Volume
	m	*mm*		*trees/ha*	*yr*	*m*	*mm*	*m²/ha*	*m³/ha*
Plantations									
Puerto Rico									
Toro Negro *(24)*	900	2500	deep, acid clay	NA[2]	5	1.1	6.4	NA	NA
Toro Negro *(25)*	900	2500	deep, acid clay	NA	9	0.2	5.1	NA	NA
Trinidad									
Central Range *(27)*	100	2000	NA	370	21	0.8	8.1	0.4	2.37
Natural stands									
Puerto Rico									
El Verde *(29)*	450	3000	deep, acid clay	700	2.5	NA	3.2	NA	NA
Sabana *(14)*	180 to 360	2300	deep, acid clay	800	17	NA	5.1	NA	NA
Rio Grande *(14)*	420 to 600	3000	deep, acid clay	800	17	NA	5.8	NA	NA
St. Just *(34)*	60	1900	shallow, acid clay	2460	2	NA	5.8	0.04	NA
	ft	*in*		*trees/acre*	*yr*	*ft*	*in*	*ft²/acre*	*ft³/acre*
Plantations									
Puerto Rico									
Toro Negro	2,950	100	deep, acid clay	NA	5	3.6	0.25	NA	NA
Toro Negro	2,950	100	deep, acid clay	NA	9	0.7	0.20	NA	NA
Trinidad									
Central Range	330	80	NA	150	21	2.6	0.32	1.74	33.86
Natural stands									
Puerto Rico									
El Verde	1,480	120	deep, acid clay	283	2.5	NA	0.13	NA	NA
Sabana	590 to 1,180	90	deep, acid clay	324	17	NA	0.20	NA	NA
Rio Grande	1,380 to 1,970	120	deep, acid clay	324	17	NA	0.23	NA	NA
St. Just	200	75	shallow, acid clay	996	2	NA	0.23	0.09	NA

[1] For natural stands, all species of trees greater than 4 cm (1.6 in) in d.b.h.
[2] Not available.

24 to 68 to 8 was found. Fibrous roots constituted 28 percent of the total root biomass *(10)*.

Reaction to Competition—Ausubo is classed as very tolerant of shade throughout most of its life. It regenerates and is capable of growing through sapling, pole, and immature stages in dense shade. Basal area and diameter growth, however, are more rapid in trees that are exposed to the sun *(29)*. In Trinidad, it was ranked second among the more valuable timber species with regard to shade tolerance *(27)*. Its slow growth in seedling stages exposes it to damage by grazing animals and results in low survival rate for the species. In Puerto Rico, ausubo has been transplanted under fairly dense shelterwood *(24)* with good survival and satisfactory growth.

Ausubo was found on each of six permanent plots measured since the mid-1940's in the Luquillo Mountains of Puerto Rico. On plots that normally contain 40 to 50 species per 0.4 hectare (1 acre), ausubo ranked 5th in density, and 10th in both basal area and volume *(6)*. Recurrent measurement of all trees on these plots revealed a 30-year chronology of stand dynamics after a hurricane. Ausubo, a primary species, increased in dominance over time, doubling its proportion of stand basal area to 10.7 percent and tripling its stand biomass to 9.1 percent *(12)*. Large size at maturity, a long life cycle, good root development, and tolerance of shade enable ausubo to persist for 300 to 400 years and emerge as one of the canopy species in the Luquillo Forest.

Damaging Agents—Survival is hampered by the very slow rate of seedling growth, and the fact that during this stage ausubo is succulent and eaten by animals *(27)*. The leaves are frequently darkened by a layer of sooty mold that probably reduces the amount of light received. In a study of microfungal populations on ausubo leaves, it was found that a statistically greater number of fungi were present on the leaves at lower levels of the canopy than at mid- and upper-levels *(11)*.

Ausubo tolerates exposure well. Along the north coast of Trinidad, several groups of trees grew in areas exposed to the full force of the northeasterly tradewinds. Marshall *(27)* observed that even the clearing of a site for the construction of a cabin, leaving numerous large ausubo isolated, apparently had no effect on their survivial.

Some infestations have been observed. In Trinidad, large trees with hollow bases were infested with both termites and a fungus, but it was not determined which agent was the primary cause of infection *(27)*. In Puerto Rico, a canker has been observed that results in the dieback of branches, but the causative agent is unknown *(33)*.

Perhaps the agent most damaging to ausubo is man. In the process of "bleeding" trees to obtain balata gum, trees may be indiscriminately slashed and later die. Sometimes they are felled to obtain the latex.

Special Uses

The heartwood is light red when cut and turns to dark reddish brown when dry. The sapwood is whitish to pale brown. The wood is very hard, strong, fine textured, and heavy, with a specific gravity of 0.85. The wood rates excellent for boring, fair for planing, and poor for turning *(21,22,23)*. It is difficult to air season and shows severe checking and warp if dried too fast *(9)*. The wood finishes very well and resembles mahogany. It is resistant to the dry wood termite, *Crytotermes brevis*, in Puerto Rico *(35)*, highly resistant to the subterranean termites, *Coptotermes niger, Heterotermes convexinotatus, H. tennis*, and *Nasutitermes corniger*, in Panama, but susceptible to marine borers. The wood is also very resistant to white- and brown-rot fungus *(7,9,23)* and is very durable in contact with the ground *(28)*.

Ausubo is one of the strongest and most attractive commercial woods in Puerto Rico. It is widely used in the tropics for railway sleepers, bridging, heavy construction, furniture, turnery, flooring, violin bows, and billiard cues. Its strength, high wear resistance, and durability qualify the timber for use in textile and pulpmill equipment *(9,21,27)*. Its excellent steam-bending properties make it suitable for boat frames and other bent work *(23)*.

The tree is also tapped for balata gum which is similar to gutta-percha. In some areas, trees have yielded sap for more than 25 years *(30)*. The latex is coagulated by fire or dried in the sun, and souvenirs or novelties are then fabricated *(21)*.

The sap from some of the species within the genus apparently can be used as a substitute for cow's milk. The latex has the consistency and taste of cream, but overindulgence in it can result in severe constipation.

Genetics

No information was found on population differences, races, or hybrids. The genus is pantropical, contains more than 150 species, and is the most important within the Sapotaceae family. Ausubo extends from latitude 23° N. to about 18° S. in the American tropics, and it is possible that varieties remain to be described.

Zapote de costa (*Manilkara pleeana*) (Pierre) Cronq. is a related tree of moist coastal forests known only from Puerto Rico, Vieques, St. John, and Tortola *(21)*. Several other closely related species of *Manilkara* grow in Central and South America and are confused with *M. bidentata* *(23)*. Much taxonomic study is needed in the Sapotaceae family, genus *Manilkara*.

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Melaleuca quinquenervia (Cav.) S. T. Blake **Melaleuca**

Myrtaceae **Myrtle family**

T. F. Geary and S. L. Woodall

Melaleuca *(Melaleuca quinquenervia)*, also known as cajeput-tree, punktree, paperbark-tree, five-veined paperbark, or bottlebrush, is an evergreen tree from Australia brought to this country as an ornamental because of its showy "bottlebrush" flowers *(3,11,12)*. It has been planted widely in tropical and subtropical regions. In Florida it has escaped cultivation and become naturalized in low areas and cypress swamps where it has an invasive habit. Any commercial use of the tree for timber products or biomass fuel is hampered by the quality of its corky bark. It is a productive honey tree, but stands of melaleuca are of dubious value to wildlife.

Habitat

Native Range

Melaleuca's native range is along the coast of eastern Australia from Sydney northward. It is native also in New Caledonia, Papua, New Guinea, and Irian Jaya. Melaleuca grows in swampy ground and on creek banks, and even on hillsides if ground water remains close to the surface. In its native habitat, melaleuca grows to 25 m (82 ft) tall and is typically found in almost pure stands or with a few associates, such as *Casuarina glauca*, *Eucalyptus robusta*, and *E. tereticornis (2,3,10,22)*.

In melaleuca's Australian habitat, soils are nutrient deficient and flooded or wet for most of the year; summer rainfall dominates; light frost (−1° to −3° C; 30° to 27° F) occurs in most years in the south; spring is associated with brief to acute water stress; and fire and water-table fluctuations are major factors governing plant distribution *(3,4,22)*. These conditions are similar to those of southern Florida *(24)* and help explain melaleuca's aggressive spread there.

In the continental United States, melaleuca is naturalized on a significant scale only in southern Florida. In Hawaii *(20)*, a million trees have been planted in Hawaii State Forest Reserves alone, but natural regeneration is very localized. Planted melaleuca is common in southern California and is occasionally found in extreme southern Texas; it is uncommon in Puerto Rico *(13)*.

Melaleuca was introduced to southern Florida in the early 1900's *(14)*. By 1980 it dominated the stands in which it grew, or, where no other trees existed, it had a minimum stocking of 17 percent on 16 000 ha (40,000 acres) *(8, p. 1-8)*. Scattered individuals and clusters of melaleuca trees grow on an additional 170 000 ha (420,000 acres) from the northern edge of Lake Okeechobee southward. Rare and isolated small pockets of natural regeneration are found in central Florida. Much of the melaleuca is in and around urban areas and it is grown as an ornamental as far north as Gainesville.

Climate

Southern Florida's climate is transitional between tropical wet-and-dry and subtropical humid and is similar to the climate of melaleuca's native habitat in Australia *(21)*. The rainy season normally begins in June and ends in September in Florida. Occasional sudden freezing temperatures, which can be expected from late November to early March *(15)*, and dry-season rainfall, both of which result from the passing of continental cold fronts, distinguish southern Florida's climate from tropical wet-and-dry.

In Hawaii, rainfall is evenly distributed or has a winter maximum. Good growth of melaleuca occurs at mean annual temperatures from 24° to 18° C (75° to 65° F), but trees grow in even cooler temperatures at high elevations *(20)*. Trees grow well in rainfall of 1020 mm (40 in) at lower elevations *(20)*, and 5080 mm (200 in) at higher elevations.

Soils and Topography

Most of southern Florida is less than 8 m (25 ft) above sea level. The land is level to very gently sloping, and a freshwater table is close to the soil surface. In general, soils supporting melaleuca are in the suborders Psammaquents, Aquods, and Saprists (sometimes marly) of the orders Entisol, Spodosol, and Histosol, respectively *(23)*. Many soils are shallow and underlain by limestone. In Hawaii, melaleuca is found from sea level to 1400 m (4,500 ft) elevation *(20)*. It grows fairly well on all Hawaiian soils, including calcareous beach sand, but does best on Inceptisols (Dystrandrepts), Ultisols, and Oxisols developed on basalt ash or lava rock of pH 4.5 to 5.5, and under rainfall of 2030 to 5080 mm (80 to 200 in) per year.

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Associated Forest Cover

Most natural vegetation of southern Florida can be invaded to some extent by melaleuca *(8,* p. 9-15). It is often found growing in the cover type Pondcypress (Society of American Foresters Type 100) and in South Florida Slash Pine (Type 111); to a lesser extent it can be found in Baldcypress (Type 101) *(6).* The ecotone between slash pine and either cypress variety is readily invaded. Melaleuca also exists in some locations with the naturalized species Brazil peppertree *(Schinus terebinthifolia)* and Australian-pine *(Casuarina* spp.). It is even found with button-mangrove *(Conocarpus erectus)* just inland of the tidal zone of Mangrove (Type 106). However, melaleuca invasion is less prominent on forested sites than on marshes and wet savannas.

Most shrub, herb, and graminoid species in southern Florida are likely to be found in association with melaleuca. Common associates are saw-palmetto *(Serenoa repens),* three-awn wiregrass *(Aristida stricta),* southern bayberry *(Myrica cerifera),* sawgrass *(Cladium jamaicense),* buttonbush *(Cephalanthus occidentalis),* and sawfern *(Blechnum serrulatum).*

In Hawaii, natural regeneration occurs only at the edges of plantations, on road cuts, and in swampy, sparsely vegetated spots in forests *(20).* It is one of the few trees that survive planting and reproduce naturally on upland bogs that form when native forests are destroyed.

Life History

Reproduction and Early Growth

Flowering and Fruiting—In Florida, flowering typically begins by age 3 and seedlings less than 1 m (3 ft) tall may bloom *(14).* Showy flowers are borne in creamy-white "bottlebrush" spikes 3 to 8 cm (1 to 3 in) long. Flowering occurs in every month except February, March, and April. After flowering, twigs continue to elongate from the ends of spikes to produce leaves or more flowers. Individual trees bloom from two to five times a year, but pronounced, regionwide flowering occurs at least twice a year. Soil type may influence time of flowering, and heavy rainfall may trigger flowering. In Hawaii, melaleuca flowers throughout the year *(20).* The species is monoecious, flowers are complete, and pollination is by insects.

Seed Production and Dissemination—Melaleuca's reproductive potential is prodigious *(14,25).* On average, 30 sessile seed capsules are left by one flower spike; a branch may bear 8 to 12 of these seed-bearing sections, often alternating with foliage, along a single axis. The capsules are hard, woody, squat, cylindrical, and brown and are aggregated in tightly packed files around the branches. A tree can hold seeds for more than 10 years. The seeds are tiny (30,000/g or 850,000/oz); a single capsule contains 200 to 350 seeds. Seeds are not released at maturity, but fire, frost, wind breakage, natural pruning, or damage by people interrupts the capsules' vascular connections, causing them to dehisce. While large numbers of seeds are typically released after injury, seedfall may occur year round. Ninety-nine percent of the seeds fall within a radius 15 times the height of the seed tree *(8,* p. 17-21). Fallen seeds can be spread by flowing water.

Seedling Development—Germination is epigeal. Dense reproduction occurs when fire prepares a seedbed and causes trees to shed millions of seeds. Seedlings averaging 2 m (6.5 ft) tall may be as dense as 3.5 million per ha (1.4 million/acre). If seedlings are submerged by water for several months, they may survive and resume growth. Seedling height growth may occur every month of the year, but growth is most rapid in spring to early summer and late summer to early fall. Natural seedlings rarely grow more than 1 m (3 ft) tall during the first year. However, seedlings planted at a density of 10,000 per ha (4,050/acre) grew 2 m (6.5 ft) in 6 months on drained muck soil *(5,7,8,* p. 23–28, *14,17).*

Vegetative Reproduction—Melaleuca stumps readily sprout, and felled tops can root under very moist conditions. Root suckering is rare but can be profuse when it occurs *(1,14).*

Sapling and Pole Stages to Maturity

Growth and Yield—The difficulty in determining ages of melaleuca trees has limited growth analyses *(7,8,* p. 23–28). A representative sapling stand may have 34,500 saplings per hectare (14,000/acre), and some areas have up to 158,000 per ha (64,000/acre). In Florida swamps, melaleuca stands that appear mature (fig. 1) may have 7,000 to 20,000 melaleuca stems per hectare (2,900 to 8,100/acre), outside bark basal area up to 133 m^2/ha (580 ft^2/acre), and a volume outside bark of 770 m^3/ha (11,000 ft^3/acre). Average heights in these stands range from 15 to 21 m (49 to 69 ft). Maximum height is 30 m (98 ft). Stands on shallow or better drained soils contain substantially less volume than the swamp stands, although the density of stems may be equally high.

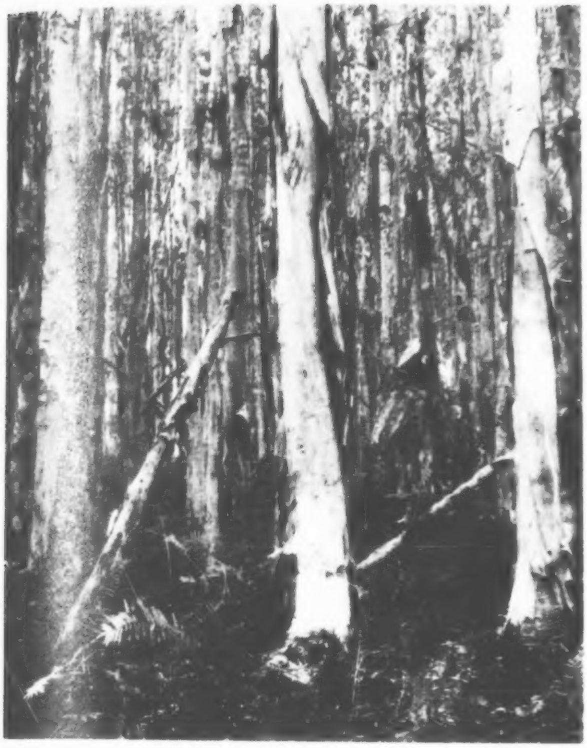

Figure 1—*A swamp stand of mature melaleuca during the dry season.*

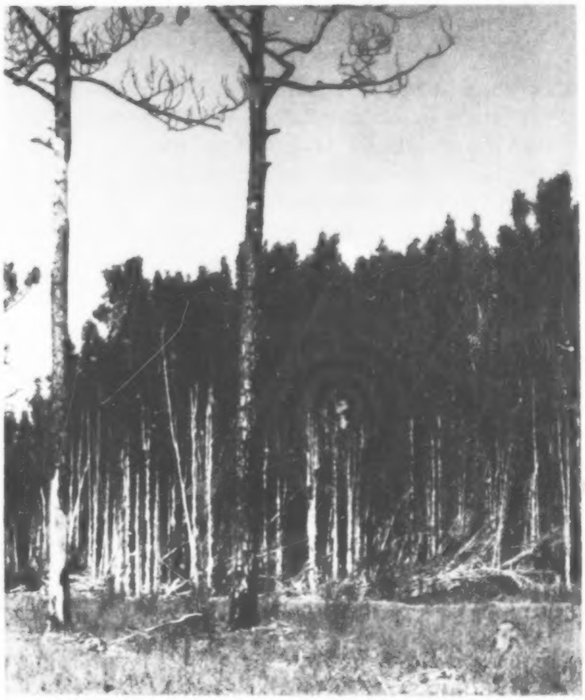

Figure 2—*Pure melaleuca stand with adjacent, fire-killed south Florida slash pine.*

Trees in Hawaiian plantations *(20)* at age 40 on good sites average 50 cm (20 in) in d.b.h. and 18 m (60 ft) tall at a spacing of 6 by 6 m (20 by 20 ft). The largest trees there reach 90 cm (36 in) in d.b.h. and 24 m (80 ft) in height.

Rooting Habit—The root system of melaleuca is adapted to fluctuating water tables. The surface root network is complemented by abundant vertical sinker roots that extend at least to the water table's deepest annual level. During periods of surface flooding, "water roots" proliferate from permanent surface roots and submerged portions of the stem *(14)*.

Reaction to Competition—Melaleuca rarely has to compete directly with other tree species in Florida because it mainly invades sparsely vegetated ecotones, prairies, marshes, and fire-damaged forests. It is classed as intolerant of shade. Melaleuca's presence in pine and cypress stands (fig. 2) can cause an otherwise innocuous fire to become a crown fire that damages melaleuca only superficially but can kill the coniferous competition *(8*, p. 29–35). Massive seed release typically follows, allowing melaleuca to preempt the site and form an almost pure stand. Pure stands with closed canopy strongly inhibit the development of understory vegetation, including advance reproduction of melaleuca seedlings.

Landscaping and lowering of water tables have accelerated the spread of melaleuca in Florida and increased the area that can be invaded easily. Melaleuca is a common ornamental in southern and central Florida; seed trees have, thereby, become widely distributed. Drainage and excessive use of ground waters shortens the annual hydroperiod, the effect being a substantial increase in large destructive wildfires *(24)*. A general drying of the environment places most native wetland plants at a disadvantage relative to melaleuca, which successfully combines the tolerance of fire and seasonally low ground water levels with adaptations to seasonal flooding. In Hawaii, fire is not common and sites with impeded drainage do not dominate; therefore, melaleuca has little competitive advantage.

Damaging Agents—Melaleuca seems to be unusually free of disease, even in its native habitat *(9,22)*. Although many insects, nematodes, and fungi have been found on melaleuca in Florida, none seriously damages the trees *(8*, p. 125–128). Severe freezes defoliate and kill branches of mature melaleuca even in extreme southern Florida, but trees generally recover by epicormic sprouting. Even when the cambium is killed to the ground line, sprouts arise from the root collar. Seedling kill from freezes, however, probably limits significant amounts of natural regeneration north of Lake Okeechobee. Melaleuca is rarely killed by fire; fire-damaged trees quickly recover by prolific epicormic sprouting.

Special Uses

In Florida, melaleuca is a common ornamental, but to many, an undesirable one because of its reputation for causing acute respiratory problems. Volatile substances produced by the tree have been implicated *(16)*. Oils in the foliage and bark emit a medicinal fragrance; the nectiferous flowers emit an unpleasant, musty odor. However, clinical studies found neither the tree's vapors nor its pollen to be virulent irritants or allergens *(8*, p. 101–115). Respiratory problems attributed to melaleuca do not occur in Australia *(10)* or in Hawaii *(20)*.

Melaleuca is not used in Florida or Hawaii for traditional timber products because its bark-to-wood ratio is high, the average stem diameter small, and the form poor. However, the wood is a suitable timber for such uses as pulp and cabinetry; the bark has potential uses as an amendment to plant potting mixes and in packaging and insulation *(8*, p. 37–68). The entire tree can be used as a biomass fuel but it is more difficult to use than most other species because of its powdery, low-density bark *(8*, p. 69–78). The leaves contain an essential oil (niaouli oil) that is extracted and sold commercially in New Caledonia *(2,19)*. The virtually identical cajeput oil is derived from *Melaleuca cajeputi* in Indonesia. In Hawaii the tree was planted to conserve soil on deforested sites, and the tree has had many other uses in its native habitat *(18,20,22)*.

The abundant flower crops of this insect-pollinated species are essential to Florida's large apiary industry *(8*, p. 79–80). However, melaleuca in Florida is viewed by many as an environmental threat that transcends its commercial value. Native vegetation is displaced and pure stands have dubious value to wildlife (*8*, p. 81–89, 91–98). Its consumption of ground water is suspected to substantially exceed that of native vegetation (*8*, p. 117–123). Buildings in melaleuca stands are exposed to a serious fire hazard (*8*, p. 29–35).

Genetics

Melaleuca was initially introduced into Florida as seeds and probably originated from only a few trees in New South Wales, Australia *(14)*. Records for these initial and possibly subsequent introductions are inadequate for determining provenance.

Racial differences have not been observed in Florida. In Hawaii, at least eight other melaleuca species are present on a minor scale *(20)*. *Melaleuca quinquenervia* for many years was lumped with nine other species under the name *M. leucadendron* (L.) L., confusing the literature considerably *(2)*.

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Metrosideros polymorpha Gaud. ‘Ohi‘a lehua

Myrtaceae Myrtle family

Ken Adee and C. Eugene Conrad

‘Ohi‘a lehua (*Metrosideros polymorpha*) is the most abundant and widespread tree in Hawaii. This slow growing native hardwood seeds freely and often starts as an epiphyte in fern forests. It is the first tree to appear on new lava flows where it offers watershed protection. The wood is of fine even texture and takes a good polish. It is used for flooring, fenceposts, and fuel. This tree provides important habitat to native birds, several endangered.

Habitat

Native Range

‘Ohi‘a lehua (fig. 1) is a variable and unusual tree found from just above sea level to 2600 m (8,500 ft) as a tree or small shrub on six of the high islands of the State. ‘Ohi‘a lehua does not grow in coastal areas with rainfall less than 500 mm (20 in). The species reaches its maximum stand basal area on young volcanic substrates in rain forest habitats on the Island of Hawaii.

Climate

Rainfall and associated cloud cover over the range of ‘ohi‘a lehua vary considerably. Mean annual precipitation varies from 500 mm (20 in) to greater than 11 400 mm (450 in). Mean annual temperatures range from 24° C (75° F) to 10° C (50° F). Seasonal variation in mean monthly temperature probably does not exceed 5° C (9° F). Frost and occasional ephemeral snow occur at higher elevations. Relative humidity commonly averages 70 to 80 percent in windward areas (exposed to northeast trade winds) and 60 to 70 percent in leeward areas.

Soils and Topography

‘Ohi‘a lehua grows on many different soils and sites. It is abundant on Histosols and Inceptisols over gently sloping recent to Pleistocene lava flows on the geologically younger volcanoes. It also is known to grow on soil associations within the soil orders Histosols, Mollisols, Spodosols, Oxisols, Ultisols, and Alfisols and on unclassified mountainous land on the geologically older volcanoes of the Hawaiian archipelago.

The species develops best on relatively level well-drained sites. On exposed ridges, steep slopes, or poorly drained sites, however, ‘ohi‘a lehua does not reach large size and may be reduced to dwarf shrub stature.

Associated Forest Cover

‘Ohi‘a lehua grows in association with many other trees in a variety of forest types but not in any classified by the Society of American Foresters. In rain forests, it is often associated with koa (*Acacia koa*), and species of ‘olapa (*Cheirodendron*), treefern (*Cibotium*), pilo (*Coprosma*), manono (*Gouldia*), kawa‘u (*Ilex*), kōlea (*Myrsine*), ‘alani (*Pelea*), guava (*Psidium*), and kōpiko (*Psychotria*) *(2,8,13)*. In drier habitats, ‘ohi‘a lehua is commonly associated with lama (*Diospyros*), ‘ākoko (*Dracaena*), wiliwili (*Erythrina*), naio (*Myoporum*), olopua (*Osmanthus*), ‘ohe makai (*Reynoldsia*), mamane (*Sophora*), hame (*Antidesma*), and maua (*Xylosma*). In many habitats, ‘ohi‘a lehua is the most common tree.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowering generally peaks in spring or summer after vegetative flushing, but some varieties or populations peak in fall or winter. Individual trees or branches may produce flowers at any time during the year. The red, salmon, pink, or yellow perfect flowers are arranged in a dense terminal cymose corymb. The stamens are long and numerous and the flowers are quite showy. Endemic Hawaiian birds (Drepanididae) and insects are the most important pollinators of ‘ohi‘a lehua. The inflorescence normally has 18 to 24 flowers in different developmental stages. Fruit maturation takes 4 to 12 months *(15)*.

Seed Production and Dissemination—Little is known about the age at which the trees begin to bear seeds or the number of seeds produced. Many small lightweight seeds may be produced per capsule, but many of these are infertile *(9)*. Seed germination is best with newly produced seeds and varies from less than 1 to 78 percent *(6)*. In a nonrandom sample of 142 trees more than 90 percent had germination

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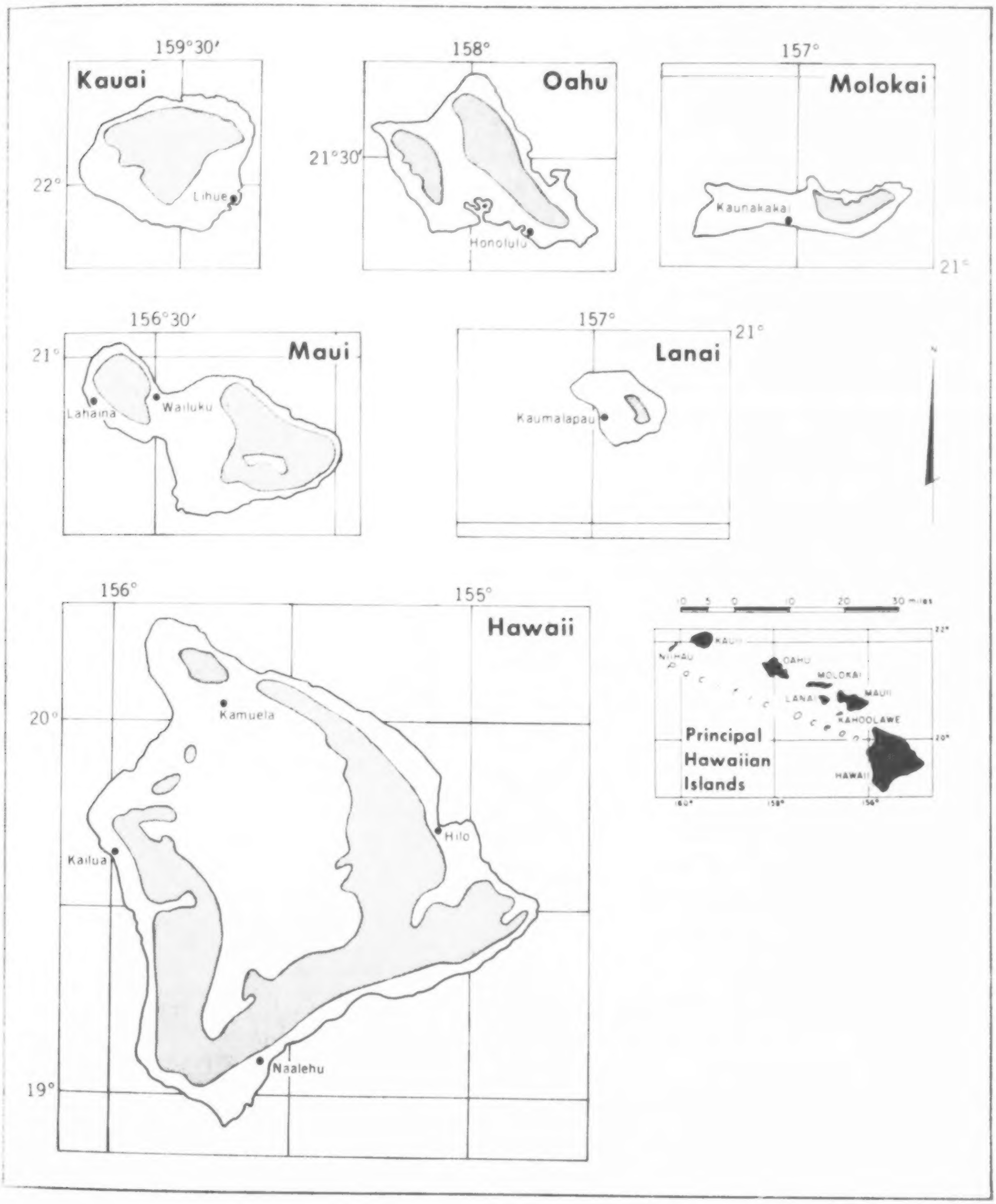
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Figure 1—*The range of 'ohi'a lehua.*

rates less than 35 percent. In one study, maximum germination of 'ohi'a lehua seed was obtained at 25° C (77° F) and 4 to 15 percent full sunlight *(2)*. Seeds remain viable for as long as 9 months if stored at room temperature *(5)*.

Seedling Development—Germination is epigeal. Many seeds germinate on downed or upright treeferns and downed moss-covered trees. More than 70 percent of the seedlings in the rain forest habitat grow on these substrates. In one 'ohi'a-treefern community a late summer peak in the appearance of 'ohi'a lehua germinants has been documented *(2)*.

Seedling growth rates are relatively slow. In one study, seedling height growth averaged less than 10 cm (4 in) per year. Survival and growth of seedlings established in shade reached a maximum at less than full sunlight after varying degrees of canopy removal *(2)*.

Vegetative Reproduction—'Ohi'a lehua often reproduces vegetatively from stem sprouts on fallen trees. The stem sprouts can produce adventitious roots and eventually become independent. Stem sprouts on a standing weakened or dying tree may outlive the parent tree and grow to maturity. Planting stock can be produced from at least 60 percent of new-growth cuttings within about 6 months compared with up to a year to produce seedlings *(4)*.

Sapling and Pole Stages to Maturity

Growth and Yield—'Ohi'a lehua is a relatively slow-growing tree. In one study (unpublished), saplings and mature trees in stands rated as commercial 'ohi'a lehua forest had a mean annual d.b.h. increment of 0.25 cm (0.10 in).

On good sites, 'ohi'a lehua commonly grows to 20 m (65 ft) and 45 cm (18 in) in diameter (fig. 2). Trees 30 m (100 ft) tall exceeding 120 cm (48 in) in diameter have been found.

'Ohi'a lehua grows in both pure and mixed stands. Stand basal area can exceed 40 m²/ha (175 ft²/acre) in pure stands on good sites. Pure stands probably are the result of disturbance.

Rooting Habit—No quantitative studies are available concerning the rooting habit of 'ohi'a lehua. Most roots apparently are near the surface. On deep soil and broken lava some deep woody roots may be formed.

Reaction to Competition—Shade tolerance of 'ohi'a lehua ranges from intolerant to intermediate, depending on varietal differences *(3,13)*.

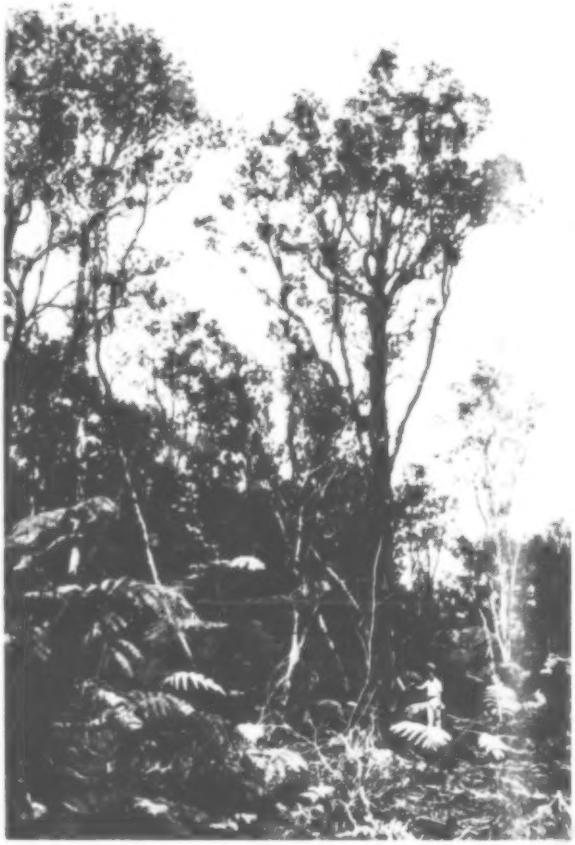

Figure 2—*A mature stand of 'ohi'a lehua on the island of Hawaii.*

A pioneer species on young volcanic substrates *(17)*, 'ohi'a lehua retains dominance on some relatively old soils. *Acacia koa* is its primary competitor for canopy dominance in wet forests. *Cibotium* spp. (treeferns) may displace 'ohi'a lehua on those sites with optimal conditions for treefern growth *(2,13)*.

Damaging Agents—Many insects attack 'ohi'a lehua trees. Among these, the endemic cerambycid borer *Plagithmysus bilineatus* has the greatest potential impact. It may become epidemic and fatal to weakened trees and is associated with extensive canopy dieback. Environmental stresses are significant in reducing 'ohi'a lehua vigor and predisposing the trees to attack by *P. bilineatus (14)*. Other potentially damaging borers are *Ceresium unicolor*, *Xyleborus saxesensi*, and *X. simillimus*. Defoliators and sapsucking insects also cause minor injury to 'ohi'a lehua.

The root rots, *Phytophthora cinnamomi (14)* and *Pythium vexans*, and the shoestring root rot, *Armillaria mellea*, can be locally damaging and also are associated with canopy dieback. Damping off caused by *Rhizoctonia* spp. also has been reported *(6)*.

Decline of 'ohi'a lehua canopy has been the subject of considerable research since 1975 showing that the phenomenon is most likely characteristic of the species. The loss of ability to withstand environmental stresses, diseases, or insect attacks is apparently synchronous among trees within populations. Entire stands of approximately equal age trees may die back to a few remanents *(1,10,11)*.

Special Uses

'Ohi'a lehua provides valuable watershed protection in Hawaii. It is also an important source of nectar and insect prey of most native birds. Among these birds are some endangered species, the ākepa *(Loxops coccinea)*, the crested honeycreeper *(Palmeria dolei)*, and several species of *Hemignathus*.

Genetics

Taxonomists recognize 11 varieties of *Metrosideros polymorpha (16,17,18)*. Only *M. polymorpha* var. *prostrata* does not attain tree stature. Intrapopulation variability of many morphological characters is large and some vegetative characteristics vary clinally with altitude *(6,7)*.

The distinction between races (ecotypes) and varieties in 'ohi'a lehua is not clear. Altitudinal *(7)*, edaphic, and successional *(13)* ecotypes have been proposed in this variable species. Some ecotypes or varieties appear to be pioneer plants in primary succession. On Mauna Loa, an active volcano, the species is found up to 2,500 m elevation, but on nearby Mauna Kea, a volcano extinct since the Pleistocene, the upper limit is about 1,650 m. On older high islands, the species seems to be limited to continuously moist rain forest environments *(12)*. Morphology of the varieties also differs; those with pubescent leaves are apparently pioneering forms of the species and glabrous leaf varieties are found in later successional stages *(19)*.

Intraspecific hybridization has been demonstrated in 'ohi'a lehua but there is some evidence of partial incompatibility *(6)*.

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Morus rubra L. Red Mulberry

Moraceae Mulberry family

Neil I. Lamson

Red mulberry *(Morus rubra)*, called moral in Spanish, is widespread in Eastern United States. It is a rapid-growing tree of valleys, flood plains, and low moist hillsides. This species attains its largest size in the Ohio River Valley and reaches its highest elevation (600 m or 2,000 ft) in the southern Appalachian foothills. The wood is of little commercial importance. The tree's value is derived from its abundant fruits, which are eaten by people, birds, and small mammals.

Habitat

Native Range

Red mulberry (fig. 1) extends from Massachusetts and southern Vermont west through the southern half of New York to extreme southern Ontario, southern Michigan, central Wisconsin and southeastern Minnesota; south to Iowa, southeastern Nebraska, central Kansas, western Oklahoma and central Texas; and east to southern Florida. It is also found in Bermuda.

Climate

Red mulberry grows under a variety of conditions. The frost-free period ranges from 150 days in New England to 330 days in southern Florida. Total annual precipitation ranges from 1000 to 2000 mm (40 to 80 in). Best growth is in moist coves and flood plains in the southern half of its natural range. Mean annual snowfall ranges from zero in Florida to 150 cm (60 in) in New York.

Soils and Topography

Red mulberry grows on a variety of moist soils at elevations below 600 m (2,000 ft). Soil orders on which red mulberry is found include Alfisols, Inceptisols, Spodosols, and Ultisols. Seeds are carried great distances by birds so trees may be found on any soil that is not too dry. Best development is on well-drained, moist soils of sheltered coves along streams *(7)*.

Associated Forest Cover

Associated species include sycamore *(Platanus occidentalis)*, American elm *(Ulmus americana)*, silver maple *(Acer saccharinum)*, and sweetgum *(Liquidambar styraciflua)* in the southern parts of its range. Toward the north red mulberry is associated with American elm, red maple *(Acer rubrum)*, boxelder *(Acer negundo)*, and white ash *(Fraxinus americana)*. It is a secondary species in succession and is seldom associated with primary invaders *(2)*. Red mulberry is listed as a minor component in three bottom-land cover types *(3)*: Cottonwood (Society of American Foresters Type 63), Sweetgum-Yellow-Poplar (Type 87), and Sugarberry–American Elm–Green Ash (Type 93). Associated understory species are roughleaf dogwood *(Cornus drummondii)*, flowering dogwood *(C. florida)*, swamp-privet *(Forestiera acuminata)*, Nuttall oak *(Quercus nuttallii)*, hawthorn *(Crataegus* spp.), and possumhaw *(Ilex decidua)*. Herbaceous vegetation associated with red mulberry includes pokeweed *(Phytolacca americana)*, stinging nettle *(Urtica dioica)*, poison-ivy *(Toxicodendron radicans)*, and greenbrier *(Smilax* spp.).

In the southern part of the range, red mulberry is often found in pastures and along borders of fields.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red mulberry is dioecious but can be monoecious, with male and female flowers on different branches of the same plants. Both male and female flowers are stalked axillary pendulous catkins and appear in April and May. The blackberry-like fruit reaches full development from June to August. Each fruit is composed of many small drupelets which develop from separate female flowers ripening together *(8)*.

Seed Production and Dissemination—Minimum seed-bearing age is usually about 10 years, but 1-year-old trees planted in an abandoned field in east Texas produced fruits at age 4 *(3)*. Optimum seed-bearing age is 30 to 85 years; the maximum is 125 years. Good seed crops occur every 2 to 3 years *(2)*. The average number of red mulberry fruits per kilogram is about 8,600 (3,900/lb); the average number of cleaned seeds per kilogram is 795,000

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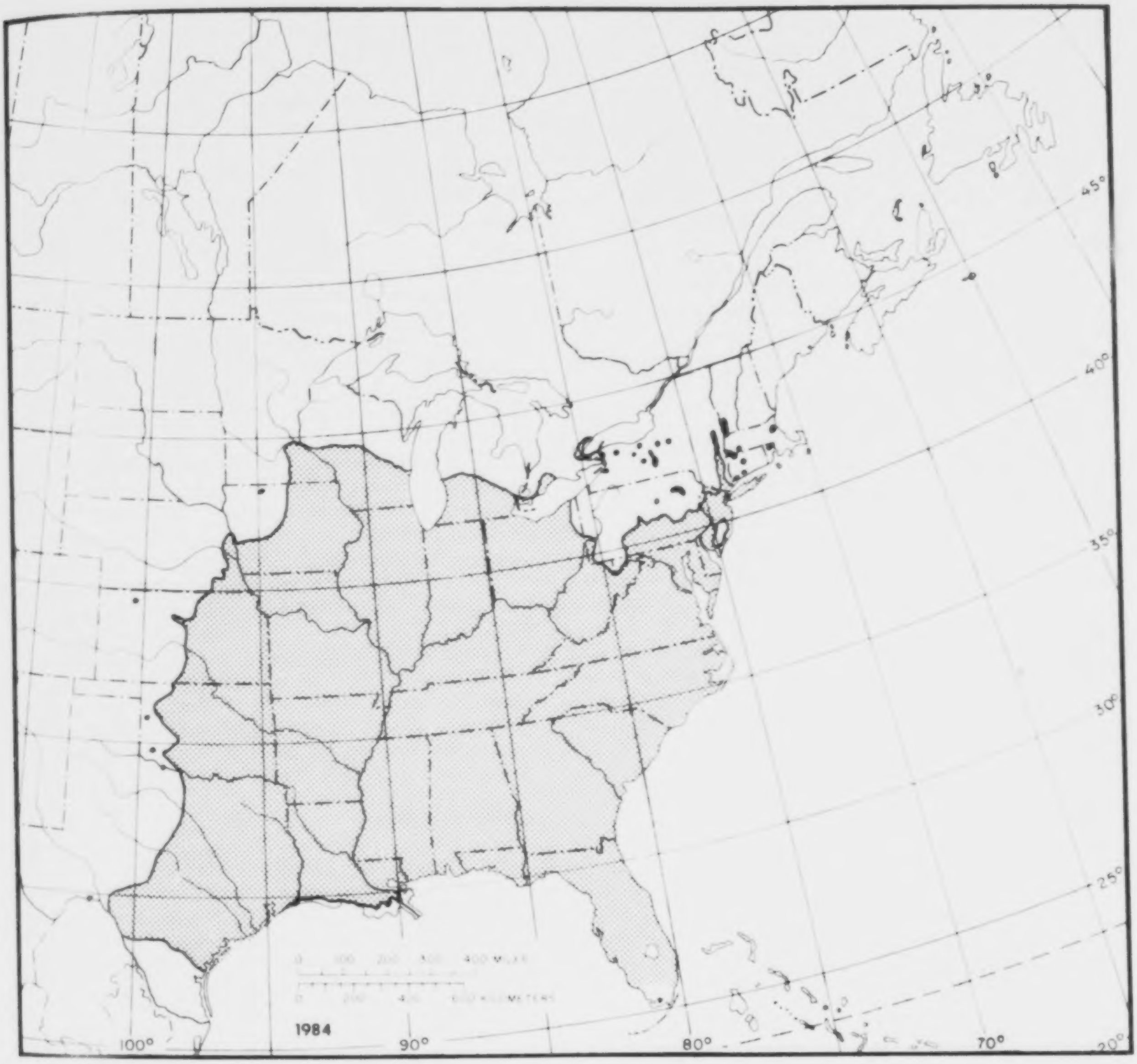
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Figure 1—*The native range of red mulberry.*

(360,000/lb). One hundred kilograms (220 lb) of fresh fruit yield 2 to 3 kg (4 to 7 lb) of cleaned seeds *(8)*.

Fruits that mature fall to the ground near the seed tree. However, because this relatively large, sweet fruit is a favorite food of most birds and some small animals, most of the fruits are eaten and dispersed by wildlife before they fully mature *(6)*.

Seedling Development—Seeds can be extracted from fresh fruits by mashing and soaking them in

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water, and then passing them through a macerator, where pulp and empty seeds are skimmed or floated off. Storage temperatures of -23° to -18° C (-10° to 0° F) are recommended for dry mulberry seeds *(8)*.

Seeds can be sown in fall without stratification or in spring following 30 to 90 days of stratification at 1° to 5° C (33° to 41° F) in moist sand. In nursery practice, seeds are sown in drills at the rate of 160 to 260/m (50 to 80/ft) in rows 20 to 30 cm (8 to 12 in) apart. Germination, which is epigeal, usually is from 12 to 50 percent. One-year bare-rooted seedlings may be outplanted *(8)*.

Vegetative Reproduction—Red mulberry can be propagated from stem cuttings or by budding, but these methods are complex and require greenhouse facilities. The average rooting from stem cuttings taken in May, September, and January was only 7 percent, regardless of time of year *(2)*. Red mulberry is a prolific root sprouter and can be reproduced by layering.

Sapling and Pole Stages to Maturity

Growth and Yield—Red mulberry (fig. 2) is usually found as scattered individuals near streams or in other moist places. Stands of any size are not mentioned in the literature. Very little is known about the growth and development of this species. At maturity, red mulberry trees are an average of 5 to 21 m (15 to 70 ft) tall and as large as 76 m (30 in) in d.b.h., depending upon habitat conditions. In wooded areas, red mulberry is often an understory tree with a rounded, spreading crown.

Rooting Habit—No information available.

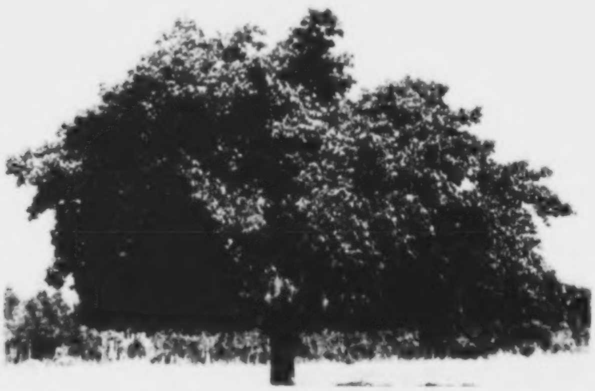

Figure 2—*Open-grown red mulberry that has been browsed by cattle.*

Reaction to Competition—Red mulberry has been planted in the Midwest because its fruits are a valuable food for wildlife, but because it provides very little soil stability or cover for wildlife it has not been planted widely *(8)*. It grows best in open conditions *(3)* but is classed as tolerant of shade as it often grows as an understory tree.

Damaging Agents—Red mulberry seems to be vanishing from at least a portion of its central range, possibly due to a bacterial disease. The effects and extent of this disease have not been investigated thoroughly, but it is known that red mulberry trees are becoming increasingly scarce *(2)*. The only noteworthy leaf pathogens of red mulberry reported in the United States are leaf spots caused by a species of *Cercospora*, *Mycosphaerella mori*, and *Pseudomonas mori (4)*. Red mulberry also is susceptible to witches' broom, *Microstroma juglandis*, but the cause is unknown.

A variety of insects feed on red mulberry leaves, including the European fruit lecanium, *Parthenolecanium corni;* Comstock mealybug, *Pseudococcus comstocki*; and cottony maple scale, *Pulvinaria innumerabilis*. The American plum borer, *Euzophera semifuneralis*, and the mulberry borer, *Doraschema wildii*, attack twigs and stems of red mulberry *(5)*.

Red mulberry has been rated as moderately tolerant of flooding as it usually withstands being inundated with up to a foot of water for a single growing season. It normally succumbs, however, after being flooded for two growing seasons *(1)*.

Special Uses

The highest use of red mulberry is for its large, sweet fruits. These are a favored food of most birds and a number of small mammals including opossum, raccoon, fox squirrels, and gray squirrels. The fruits also are used in jellies, jams, pies, and drinks. In the past, the fruits were valued for fattening hogs and as poultry food.

Red mulberry is used locally for fenceposts because the heartwood is relatively durable. Other uses of the wood include farm implements, cooperage, furniture, interior finish, and caskets *(7)*.

Genetics

Red mulberry hybridizes frequently with white mulberry *(Morus alba)*, a native of China which has become naturalized throughout parts of the Eastern United States.

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Nyssa aquatica L. Water Tupelo

Cornaceae Dogwood family

R. L. Johnson

Water tupelo (*Nyssa aquatica*), also called cottongum, sourgum, swamp tupelo, tupelo-gum, and water-gum, is a large, long-lived tree that grows in southern swamps and flood plains where its root system is periodically under water. It has a swollen base that tapers to a long, clear bole and often occurs in pure stands. A good mature tree will produce commercial timber used for furniture and crates. Many kinds of wildlife eat the fruits and it is a favored honey tree.

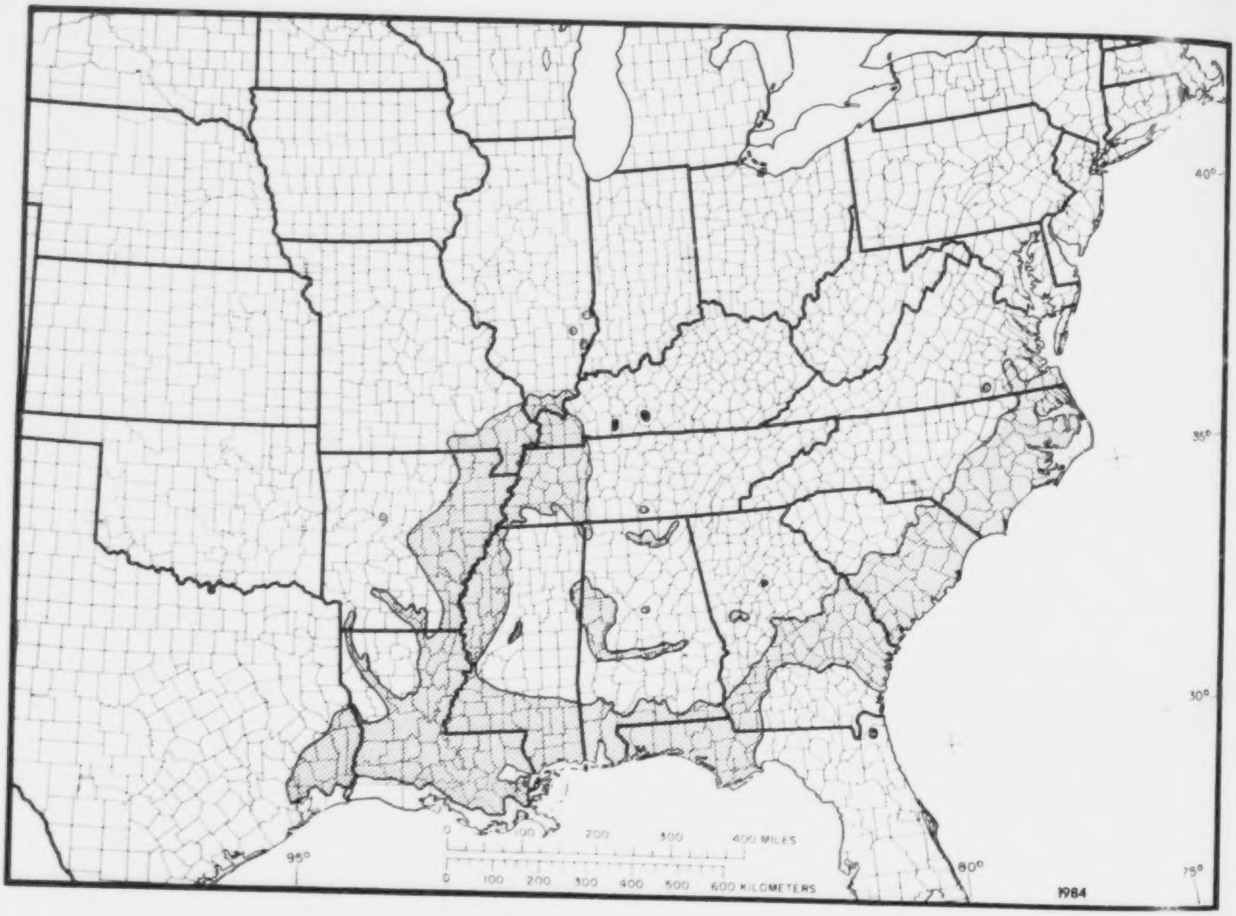
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Figure 1—*The native range of water tupelo.*

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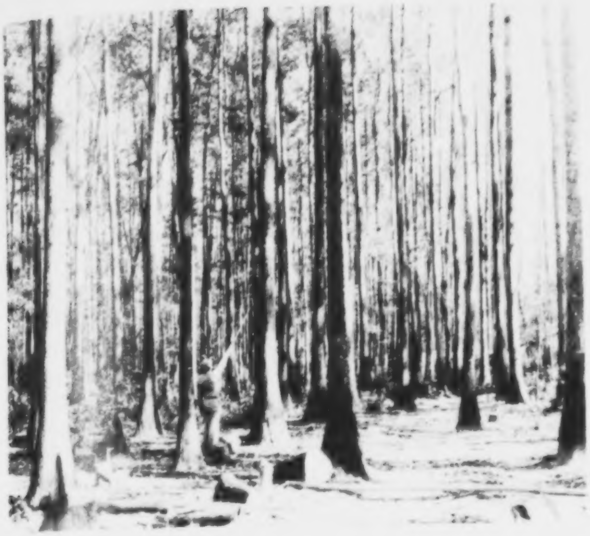

Figure 2—*Water tupelo in Attala County, MS. Before thinning, the stand averaged 53 m^2/ha (230 ft^2/acre) of basal area and 434 m^3/ha (6,200 ft^3/acre) of volume. Trees averaged 30 cm (12 in) in d.b.h. and were up to 30 m (100 ft) tall.*

Habitat

Native Range

Water tupelo (figs. 1,2) grows throughout the Coastal Plain from southeastern Virginia to southern Georgia, and from northwestern Florida along the Gulf of Mexico to southeastern Texas. It extends up the Mississippi River Valley as far north as the southern tip of Illinois.

Climate

Annual rainfall throughout the range of water tupelo averages 1320 mm (52 in). Approximately 530 mm (21 in) of rain falls during the primary growing season, April through August. Summer months are normally much drier in the Midsouth *(22)*.

Average summer temperature within the range of water tupelo is 27° C (81° F); average winter temperature is 7° C (45° F). Temperature extremes are 46° to –29° C (115° to –20° F). An average of 231 frost-free days occur annually over its range.

Soils and Topography

Water tupelo grows in low, wet flats or sloughs and in deep swamps. Some of the better sites are in the sloughs and swamps along Coastal Plain rivers of the Southeast, such as the Roanoke and Santee, and in the large swamps of southwestern Louisiana and southeastern Texas. On some sites water may reach a depth of 6 m (20 ft) during rainy seasons and may remain as high as 4 m (13 ft) for long periods *(21)*. Surface water may disappear from water tupelo areas in midsummer or fall, but on better sites soil moisture remains at or near saturation level throughout most of the growing season.

Soils that commonly support water tupelo range from mucks and clays to silts and sands and are in the orders Alfisols, Entisols, Histosols, and Inceptisols. Most are moderately to strongly acidic; subsoil frequently is rather pervious. Site index of water tupelo for several Midsouth soils ranges from 21 to 27 m (70 to 90 ft) at 50 years *(4)*.

Associated Forest Cover

Water tupelo is a major component of the forest cover types Water Tupelo–Swamp Tupelo (Society of American Foresters Type 103) and Baldcypress–Tupelo (Type 102) *(8)*. In stands containing baldcypress *(Taxodium distichum)* and water tupelo, baldcypress is usually predominant. In sloughs and moving water, water tupelo usually occupies the deeper parts and baldcypress the margins and more shallow parts. In deep, stagnant water the two species occupy much the same depths *(19)*.

In several other forest cover types water tupelo may be a minor associate: Longleaf Pine–Slash Pine (Type 83), Slash Pine (Type 84), Slash Pine–Hardwood (Type 85), and Baldcypress (Type 101).

Species associated with water tupelo throughout its range are black willow *(Salix nigra)*, swamp cottonwood *(Populus heterophylla)*, red maple *(Acer rubrum)*, waterlocust *(Gleditsia aquatica)*, overcup oak *(Quercus lyrata)*, water oak *(Q. nigra)*, water hickory *(Carya aquatica)*, green and pumpkin ash *(Fraxinus pennsylvanica* and *F. profunda)*, and sweetgum *(Liquidambar styraciflua)*. Swamp tupelo *(Nyssa sylvatica* var. *biflora)*, pondcypress *(Taxodium distichum* var. *nutans)*, and redbay *(Persea borbonia)* are common associates in the Southeast.

Small tree and shrub associates of water tupelo include swamp-privet *(Forestiera acuminata)*, common buttonbush *(Cephalanthus occidentalis)*, water-elm *(Planera aquatica)*, sweetbay *(Magnolia virginiana)*, Carolina ash *(F. caroliniana)*, poison-sumac *(Toxicodendron vernix)*, southern bayberry *(Myrica cerifera)*, and dahoon *(Ilex cassine)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Water tupelo is polygamo-dioecious. The minute, greenish-white flowers appear before or with the leaves in March or April. Pollen is disseminated by wind and probably by bees. Fruits are oblong drupes about 1 to 4 cm (0.5 to 1.5 in) long, with a thick epicarp and fleshy mesocarp. When mature, September through December of the first year, they are dark purple with conspicuous pale dots. Each fruit contains a boney, ribbed, one-seeded stone. Stones range in color from white to dark brown or gray and some are pinkish white. There are about 990 cleaned seeds per kilogram (2.2 lbs) *(30)*.

Seeds may be sown in fall in the nursery or may be stratified over winter and sown in the spring. For stratifying, seeds are kept in moist sand or plastic bags at 2° to 4° C (35° to 40° F) *(30)*. Up to 30 months' storage does not reduce viability of seeds that have a moisture content of 20 percent or less and are kept in polyethylene bags at a temperature of about 3° C (38° F) *(3)*.

Nursery-sown seeds may be drilled 13 to 25 mm (0.5 to 1 in) deep at the rate of 50/m (15/ft) of row, or they may be broadcast and rolled into the soil. A seedbed density of 110 to 165 seedlings/m^2 (10 to 15 seedlings/ft^2) is recommended. From 25 to 37 mm (1 to 1.5 in) of sawdust mulch is recommended for broadcast seeds.

Seed Production and Dissemination—Forest trees initiate seed production in about 30 years or when they are about 20 cm (8 in) in d.b.h. In a South Carolina study, however, viable seeds were produced by 2-year-old stump sprouts *(27)*. Large trees normally produce good to excellent crops each year. Seeds are dispersed mainly by water. As long as the exocarp is intact, the fruit will float. Seeds submerged continuously in water may remain viable for at least 14 months *(1)*.

Seedling Development—Germination is epigeal. Seeds do not germinate until water recedes, which may be midway to late in the growing season *(29)*. Partially shaded, wet, poorly-drained soils provide the best seedbed. Seeds buried 1 to 3 cm (0.5 to 1 in) deep in the soil have a better chance to germinate and establish seedlings than seeds on the soil surface. Seedling survival and development are best in full sunlight and in soil with a pH below 7.0 *(25)*. Seedling development is better in saturated than in well-drained soil, in moving and aerated rather than stagnant water, and in shallow rather than deep water *(6,7,11,17)*. Provided their tops are above water, seedlings can generally survive continuous flooding even if it persists throughout the growing season. Water tupelo is able to survive where it is too wet for most other species because of anatomical and physiological adaptations such as roots that allow for oxidation of the rhizosphere and controlled anaerobic respiration *(12,18)*.

Vegetative Reproduction—Water tupelo is a prolific stump sprouter. Stumps of cut seedlings 15 cm (6 in) above ground level may be better sprouters than those 1 cm (0.5 in) in height. Sprouts develop adventitiously from the higher stumps and from suppressed buds on lower stumps *(14)*. Survival and development of sprouts from stumps of larger trees are not always satisfactory, and it may be that the occurrence and persistence of stump sprouts are related to timing and duration of flooding. In South Carolina, trees of sprout origin grew as well as seedlings over a 30-year period *(16)*, but in southern Louisiana few stump sprouts survived beyond 6 years *(20)*.

There are no practical techniques for reproducing water tupelo through cuttings or layering.

Sapling and Pole Stages to Maturity

Growth and Yield—Growing season flooding that is just short of continuous may provide near-optimum soil moisture for growth of water tupelo *(2)*. Any drastic change in normal water levels can decrease growth. On a good site in South Carolina, 30-year-old trees of sprout and seed origin averaged about 23 m (75 ft) tall and 33 cm (13 in) in diameter *(16)*. (Note: determination of tree age may be difficult because the species is known to have false rings.) With an abundance of sunlight, trees growing on a good site for 50 to 75 years may reach 51 to 66 cm (20 to 26 in) in diameter above the butt swell, contain from 2 to 3.5 4.9-m (16 ft) logs, and begin development of heartwood *(2)*.

In poorly drained swamps in the southeastern United States, average annual production of water tupelo stands was found to be between 6.3 and 7.0 m^3/ha (90 and 100 ft^3/acre). Ten-year average diameter growth for trees free to grow in unmanaged stands on an average site is about 8 cm (3 in) *(28)*. Growth and yield were tabulated at 10-year intervals for unmanaged stands in the Atchafalaya Basin of southern Louisiana as follows *(9)*:

Age	Average d.b.h.	Height	Total merchantable volume (peeled wood)
yr	*cm*	*m*	*m³/ha*
30	16.8	14	156
40	24.1	17	243
50	42.2	25	331
	in	*ft*	*ft³/acre*
30	6.6	46	2,225
40	9.5	56	3,475
50	16.6	81	4,725

Under management, a pure even-aged stand carried to 107 cm (42 in) in diameter above the bottleneck is estimated to have an accumulative total yield of 676 m³/ha (48,282 mbf/acre, Doyle log rule) in logs and 441 m³/ha (70 cords/acre). These yields are based on an assumed cutting cycle of from 8 to 15 years *(28)*.

Basal areas between 57 and 69 m²/ha (250 and 300 ft²/acre) are not uncommon in pure unmanaged second-growth stands. For a less dense water tupelo stand in Florida, the following volumes were recorded *(24)*:

Age	Average diameter above bottleneck	Total merchantable volume (outside bark)	Basal area
yr	*cm*	*m³/ha*	*m²/ha*
60	31.8	355	38.6
70	34.8	429	44.5
	in	*ft³/acre*	*ft²/acre*
60	12.5	5,077	168
70	13.7	6,133	194

Table 1—Root characteristics of swamp tupelo and water tupelo as affected by drainage *(13)*

Root characteristic	Roots well aerated	Roots flooded
Morphology	Small diameter and fibrous except at the apex	Succulent with very little branching
Epidermis	Highly suberized	Little or no suberization
Endodermis	Highly organized, with Casparian strips	Poorly organized. Casparian strips not evident
Adventitious water root	None	Prolific just below water line[1]
Intercellular space in cortex	Abundant	Abundant
Oxidized rhizosphere in anaerobic conditions	No	Yes

[1] May be absent on water tupelo under many types of flooding

Growth and yield of water tupelo in plantations are generally unknown. One small 17-year-old planting at a 1.7 by 1.7 m (5.5 by 5.5 ft) spacing on Falaya silt loam had 89 percent survival. The trees that grew best averaged 13.2 cm (5.2 in) in d.b.h. and were 14.9 m (49 ft) tall *(5)*.

Rooting Habit—Water tupelo commonly grows in saturated soils where its shallow root system is characterized by morphological and physiological adaptations that are essential to survival and growth (table 1).

Reaction to Competition—Water tupelo is classed as intolerant of shade. It will survive codominant but not overtopping competition. Water tupelo develops in pure, very dense, second-growth stands and has a tendency to stagnate. Unless stagnation is prolonged, it responds to thinning.

Damaging Agents—Fire is a major enemy of water tupelo. It scorches the thin bark, allowing entrance of rot-causing fungi. The forest tent caterpillar (*Malacosoma disstria*) is a serious enemy in some years and locations. More than 202,350 ha (500,000 acres) of trees along the gulf coast from Louisiana through Alabama have been defoliated by this insect in a single year *(26)*. Trees annually defoliated seldom die but may have 30 percent or less of the annual diameter growth of unattacked trees.

A foliar disease, *Mycosphaerella nyssaecola*, has caused premature defoliation, but impact has been negligible.

Special Uses

Since water tupelo is one of the few species that can survive extended periods of inundation, it is favored for planting in very wet microsites, around buildings, in parks, and elsewhere. It is also an important wildlife species. The fruit is consumed by wood ducks, several other kinds of birds, and by squirrels, raccoons, and deer *(10)*. Flowers have some value as a source of tupelo honey. Deer feed on foliage, twigs, and stump sprouts.

Water tupelo wood has fine, uniform texture and interlocked grain. When dried properly, the lumber is used for boxes, pallets, crates, baskets, and furniture. Buttresses of trees growing in flooded areas contain wood that is much lighter in weight than that from upper portions of the same trees. The butt portion is probably best suited for pulping products *(23)*.

Genetics

There is considerable variation in specific gravity and fiber length among stands, between trees within a stand, and within individual trees. Depending on seed source, seedlings grown under similar water regimes have different rates of development *(15)*.

No racial variations or hybrids have been recognized for forest-grown water tupelo.

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Nyssa ogeche Bartr. ex Marsh. Ogeechee Tupelo

Cornaceae Dogwood family

Susan V. Kossuth and Robert L. Scheer

Ogeechee tupelo *(Nyssa ogeche)*, also called Ogeechee-lime, sour tupelo-gum, white tupelo, and bee-tupelo *(3)*, is a scarce small tree or much branched shrub found along rivers and swamps of the Coastal Plain in constantly wet soils that are often flooded. The wood is of little value, but the mature fruits and their juice are used by people. It is also an important honey tree.

Much of the information given here was contributed by L. T. Nieland, formerly State Extension Forester, Gainesville, FL, who observed Ogeechee tupelo for many years in its natural habitat and experimented with its cultivation for farm use.

Habitat

Native Range

Ogeechee tupelo (figs. 1, 2) requires a very moist site and is distributed along the borders of rivers, swamps, and ponds that are frequently inundated *(2,4)*. It grows naturally from the borders of South Carolina near the coast through the Ogeechee Valley in Georgia to Clay County in northern Florida and Washington County in western Florida *(4)*. It is found in abundance along the Ogeechee, Altamaha, and Suwannee Rivers *(2)*, and in certain wet flatwood regions between the Choctawhatchee and Wakulla Rivers of Florida *(5)*. In its Florida range it is less than 1 percent of the woody plant population.

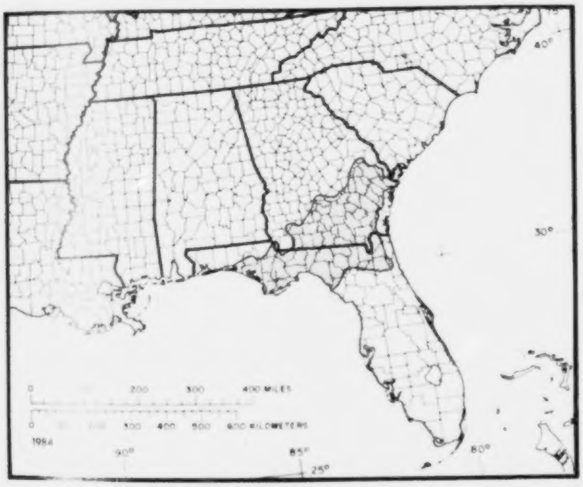

Figure 1—*The native range of Ogeechee tupelo.*

Figure 2—*Ogeechee tupelo.*

Climate

The climate over the entire range is humid to subhumid. About one-half of the 1295 mm (51 in) annual rainfall occurs between April and August. Average July and January temperatures are about 28° C (83° F) and 11° C (52° F), respectively. Extreme temperatures average approximately −22° C (−8° F) in winter and 41° C (106° F) in summer. The growing season is about 270 days.

The authors are formerly Chief Plant Physiologist and Deputy Station Director (retired), Southeastern Forest Experiment Station, Asheville, NC.

Soils and Topography

Ogeechee tupelo is limited to alluvial soils along the rivers and in river swamps. A permanently wet site is apparently requisite for satisfactory regeneration and growth. It grows successfully on soils that are flooded for long periods; however, there must be at least a slight movement of the water. Ogeechee tupelo is most commonly found growing on soils of the order Inceptisols.

Where waters back up and stand for long periods after the main flood has subsided, as in second bottoms, Ogeechee tupelo is usually a tall, deliquescent shrub or a dwarfed tree. It seldom attains tree form very far from natural stream channels. Generally it grows best and is most abundant at an elevation of only a few centimeters above the average water level and is infrequently found more than 0.3 to 0.6 m (1 to 2 ft) above the average water level of the streams along which it grows.

Associated Forest Cover

Ogeechee tupelo occurs as a minor component in the forest cover types Baldcypress–Tupelo (Society of American Foresters Type 102) and Water Tupelo–Swamp Tupelo (Type 103) *(1)*.

Associated tree species include tupelo *(Nyssa* spp.), ash *(Fraxinus* spp.), oak *(Quercus* spp.), hickory *(Carya* spp.), elm *(Ulmus* spp.), baldcypress *(Taxodium* spp.), pine *(Pinus* spp.), red maple *(Acer rubrum)*, black willow *(Salix nigra)*, swamp cottonwood *(Populus heterophylla)*, water-elm *(Planera aquatica)*, waterlocust *(Gleditsia aquatica)*, leucothoe *(Leucothoe* spp.), sweetgum *(Liquidambar styraciflua)*, persimmon *(Diospyros virginiana)*, sweetbay *(Magnolia virginiana)*, redbay *(Persea borbonia)*, and Atlantic white-cedar *(Chamaecyparis thyoides)*. Other associates may include hawthorn *(Crataegus* spp.), buttonbush *(Cephalanthus* spp.), holly *(Ilex* spp.), lyonia *(Lyonia* spp.), clethra *(Clethra* spp.), swamp-privet *(Forestiera acuminata)*, swamp dogwood *(Cornus stricta)*, swamp cyrilla *(Cyrilla racemiflora)*, poison-sumac *(Toxicodendron vernix)*, southern bayberry *(Myrica cerifera)*, and swamp rose *(Rosa palustris)*. Woody vines associated with the forest type include greenbrier *(Smilax* spp.), southeast decumaria *(Decumaria barbara)*, crossvine *(Bignonia capreolata)*, peppervine *(Ampelopsis arborea)*, supplejack *(Berchemia scandens)*, and poison-ivy *(Toxicodendron radicans)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The species is polygamo-dioecious, bearing perfect and pistillate flowers on female trees and only staminate flowers on male trees. The flowers appear from late March to early May after the new leaves are fully grown *(5)*. The minute flowers, originating in the axils of bud scales, are greenish yellow and inconspicuous with rounded to oblong petals. Pistillate flowers are solitary on short, 1.6 mm (0.06 in) woody peduncles with a deep cup-shaped woolly calyx. The style is stout, exserted (extending beyond the petals) and reflexed from near the base; remnants of it persist on the mature fruit. The male flowers occur in clusters on slender hair peduncles 1.3 mm (0.05 in) long. The filaments are inserted under the margin of a thick disk and bear oval, roughened anthers *(4)*. The male flowers, in particular, produce an abundance of nectar. Bees are extremely active in the trees during the flowering period and probably are responsible for pollen dissemination.

The fruit is an edible, oblong-shaped red drupe, 3 to 4 cm (1.0 to 1.5 in) long, containing an acid flesh. Each drupe contains one, rarely two, 3 cm (1 in) long seed with a papery, pale seedcoat. Ogeechee tupelo has the largest fruit in the genus. It matures in July and August but persists until November and December after the leaves have fallen *(4)*.

Seed Production and Dissemination—The species is a prolific and fairly consistent producer of blossoms and fruit, although a freeze after the flowers have opened may cause an occasional failure. Little is known about the age or size at which trees begin to bear seed. Seedlings planted on a lake shore in Florida grew to a height of almost 2.4 m (8 ft) in 3 years and matured a good crop of fruit at that time.

The fruit falls to the ground and into the water beneath the parent tree, and most seed dissemination is undoubtedly quite local. Birds and small animals may carry seed some distance, however. Some seed is waterborne, as drifts of the fruit may be found at previous high waterlines following floods. Fresh, undamaged fruit and the seeds from it usually sink in water *(5)*. Fruit and seeds that have dried a little will float. Cleaned seed range from 2,290 to 3,130/kg (1,040 to 1,420/lb), averaging 2,710/kg (1,230/lb).

Seedling Development—Germination is epigeal *(6)*. Data on the establishment and early growth of Ogeechee tupelo are lacking. Where the surface soil becomes very dry, the newly germinated seedlings generally do not survive. In a dense grass sod, the young trees may survive but grow very slowly.

Under favorable conditions seedlings have attained a height of 0.6 cm (2 ft) or more during the first growing season. One group of about 200 seedlings left in nursery rows along a lake shore in north Florida averaged 1.2 to 1.8 m (4 to 6 ft) in height after 2 years.

Vegetative Reproduction—Much reproduction occurs as sprouts from stumps or root crowns. Stream edges may be quite densely covered with Ogeechee tupelo that has reproduced almost exclusively by this means. There is no recorded information about propagation by cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—While Ogeechee tupelo may mature as a shrub only a few feet tall or as a 19.8 m (65 ft) tree, it is most frequently a small, crooked, deliquescent tree 7.6 to 10.7 m (25 to 35 ft) tall *(3,5)* with a narrow, round-topped crown *(4)*. Its height seldom exceeds 15.2 m (50 ft). Individual stems may have diameters of 30 to 61 cm (12 to 24 in) *(3)* but they are usually not more than 38 cm (15 in) *(5)*. The bark is 3.2 mm (0.125 in) thick, irregularly fissured, with a dark-brown surface broken into persistent platelike scales *(4)*.

The trees are probably short lived, although reliable information is lacking. When the original stems weaken or die, sprouts develop from their root crowns. These evidently produce a vigorous root system of their own, thus prolonging the life of the individual tree for a considerable time and resulting in the thicketlike growth frequently seen.

Reaction to Competition—Ogeechee tupelo is classed as intolerant of shade.

Rooting Habit and Damaging Agents—No published information is available on rooting habit or damaging agents of Ogeechee tupelo.

Special Uses

Thousands of hectares of Ogeechee tupelo have been planted in bee farms along the lower Apalachicola River and around swamps where it grows naturally *(2,4)*. Bees use nectar from the trees to make "tupelo honey." The mature fruit, known as Ogeechee lime, has a subacid flavor. It is made into preserves and is also used in making a beverage *(2)*.

The wood is light (specific gravity of 0.46), soft, tough but not strong. It is coarse grained, difficult to split, and of little value *(4)*.

Genetics

There are no known races or hybrids of Ogeechee tupelo, and genetic studies of the species have not been pursued.

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Nyssa sylvatica Marsh. Black Tupelo

Cornaceae **Dogwood family**

N. sylvatica Marsh. var. sylvatica Black Tupelo (typical)

Charles E. McGee

N. sylvatica var. biflora (Walt.) Sarg. Swamp Tupelo

Kenneth W. Outcalt

Black tupelo (*Nyssa sylvatica*) is divided into two commonly recognized varieties, typical black tupelo (var. *sylvatica*) and swamp tupelo (var. *biflora*). They are usually identifiable by their differences in habitats: black tupelo on light-textured soils of uplands and stream bottoms, swamp tupelo on heavy organic or clay soils of wet bottom lands. They do intermingle in some Coastal Plain areas and in those cases are hard to differentiate. These trees have moderate growth rate and longevity and are an excellent food source for wildlife, fine honey trees, and handsome ornamentals.

BLACK TUPELO

Black tupelo (*Nyssa sylvatica* var. *sylvatica*) is also widely known as blackgum; other common names include sourgum, pepperidge, tupelo, and tupelo-gum.

Habitat

Native Range

Black tupelo (figs. 1, 2) grows in the uplands and in alluvial stream bottoms from southwestern Maine to New York, to extreme southern Ontario, central Michigan, Illinois, and central Missouri, and south to eastern Oklahoma, eastern Texas, and southern Florida. It is local in central and southern Mexico. Optimum development is made on lower slopes and terraces in the Southeastern United States.

Climate

Due to its wide distribution, black tupelo is found in a variety of climates with a wide range of temperatures. Rainfall throughout the range averages about 1270 mm (50 in) per year. In the South and Southeast, more than half of the rain falls during the growing season while in the northerly and westerly extremes of the range, substantially less than half of the rain falls during the growing period.

Soils and Topography

Black tupelo is found on a wide variety of sites from the creek bottoms of the southern coastal plains to altitudes of 910 m (3,000 ft) in North Carolina. The variety grows best on well-drained, light-textured soils on the low ridges of second bottoms and on the high flats of silty alluvium. In the uplands it grows best on the loams and clay loams of lower slopes and coves. When found on drier upper slopes and ridges, it is seldom of log size or quality *(8)*. Approximately two-thirds of the species range is dominated by soils of the order Ultisols, with Udults as the principal suborder.

Associated Forest Cover

Black tupelo is not predominant in any major forest type; however, it is a component of 35 forest cover types *(3)*. In New England it is associated with Black Ash–American Elm–Red Maple (Society of American Foresters Type 39). In the central and southern forest regions, it is found in the following types:

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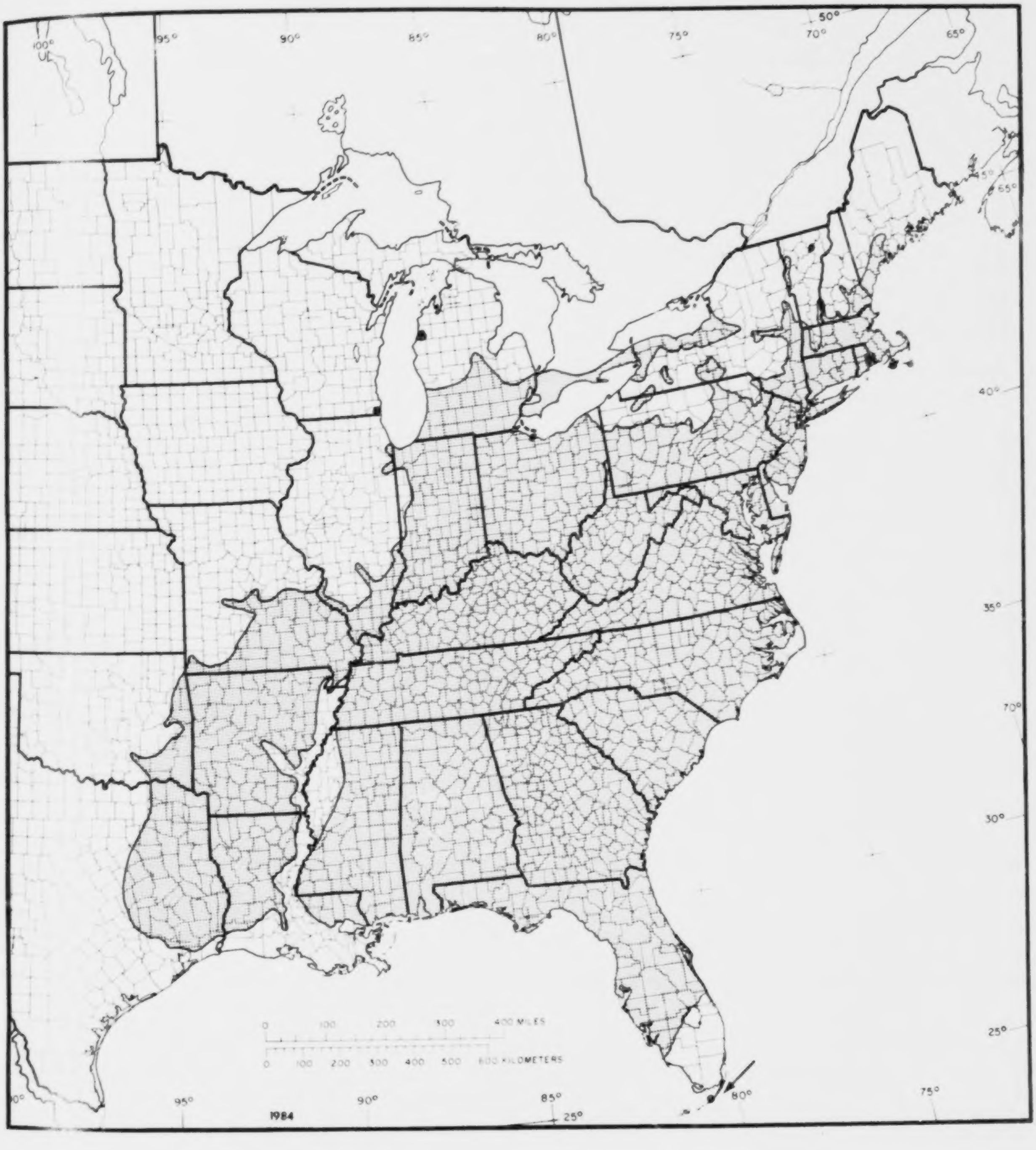
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95°
1984
90°
85°
25°
80°
75°

Figure 1—*The native range of black tupelo* (Nyssa sylvatica).

40	Post Oak-Blackjack Oak
43	Bear Oak
44	Chestnut Oak
45	Pitch Pine
46	Eastern Redcedar
51	White Pine-Chestnut Oak
52	White Oak-Black Oak-Northern Red Oak
53	White Oak
55	Northern Red Oak
57	Yellow-Poplar
58	Yellow-Poplar-Eastern Hemlock
59	Yellow-Poplar-White Oak-Northern Red Oak
65	Pin Oak-Sweetgum
70	Longleaf Pine
75	Shortleaf Pine
76	Shortleaf Pine-Oak
78	Virginia Pine-Oak
79	Virginia Pine
80	Loblolly Pine-Shortleaf Pine
81	Loblolly Pine
82	Loblolly Pine-Hardwood
83	Longleaf Pine-Slash Pine
85	Slash Pine-Hardwood
87	Sweetgum-Yellow-Poplar
91	Swamp Chestnut Oak-Cherrybark Oak
93	Sugarberry-American Elm-Green Ash
97	Atlantic White-Cedar
100	Pondcypress
104	Sweetbay-Swamp Tupelo-Redbay
110	Black Oak

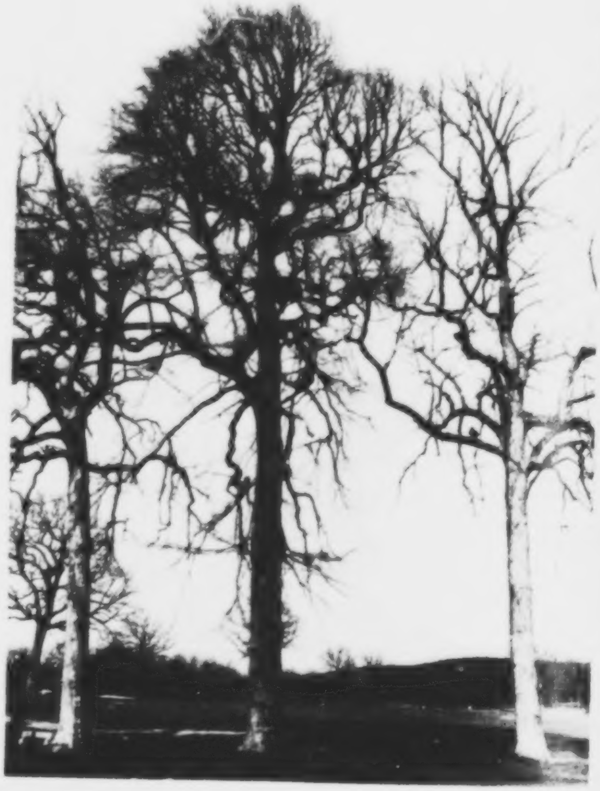

Figure 2—*Black tupelo (center).*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Black tupelo is polygamo-dioecious and flowers from April through June. The fruit of black tupelo ripens in September and October and drops from September through November. The flowers are small and greenish white, borne singly or in capitate clusters. The fruit, an oblong drupe, is about 13 mm (0.5 in) long and is blue-black; the pit is indistinctly ribbed *(2)*.

Seed Production and Dissemination—Seed production in black tupelo is highly variable. Seeds are disseminated by gravity, animals, and birds *(2)*.

Seedling Development—Under natural conditions, seeds overwinter on cool moist soil and germinate in the spring. Germination is epigeal *(2)*. Black tupelo requires nearly full light for optimum development. In a mature hardwood forest on a good site in Tennessee, 830 black tupelo/ha (337/acre) were well distributed over a 24/ha (60/acre) area. Two years following clearcutting there were 1,880 black tupelo/ha (760/acre) less than 1.37 m (4.5 ft) in height, and 375/ha (150/acre) more than 1.37 m (4.5 ft) tall. In four good young hardwood stands in northern Alabama, black tupelo ranged from 1,790 to 2,965 stems/ha (725 to 1,200/acre) 5 or 6 years after clearcutting. When three of the areas were burned as part of a controlled experiment, the number of small tupelo per hectare approximately doubled the first year; the number of stems taller than 1.37 m (4.5 ft) decreased by about 50 percent *(5)*.

Vegetative Reproduction—Smaller black tupelo stumps sprout readily and larger stumps sprout occasionally. Root suckering can occur in profusion around some trees. Layering has been used to produce black tupelo stock.

Sapling and Pole Stages to Maturity

Growth and Yield—Black tupelo can achieve heights of 36 m (120 ft) and diameters up to 122 cm (48 in) at breast height on the most favorable sites. Diameter growth on medium sites where the tree has good stand position may reach 10 to 20 cm (4 to 5 in) in 10 years. On poorer sites or where the tree is crowded, diameter and height growth can be very slow (7). Black tupelo growing on good sites that have not been burned can produce veneer logs. Most logs suitable for veneer are about 50 cm (20 in) in d.b.h. Black tupelo produces a pronounced ribbon figure and is often quarter sliced *(6)*. The light, uniform-textured wood of tupelo makes excellent containers. Much of the merchantable upland black tupelo is used for crossties and pallets. A majority of stems are not considered desirable growing stock and are often left standing following commercial timber sales. These stems are usually moderately easy to control with herbicides.

Rooting Habit—No information available.

Reaction to Competition—Black tupelo is usually found in mixture with other species. It is classed as tolerant of shade. Only rarely does it attain a dominant crown position within its age group; it usually occupies an intermediate crown position on most sites. Some intermediate black tupelo stems respond favorably to release from overtopping vegetation. Seedlings grow slowly under a fully stocked stand. When the canopy is removed, about 25 percent or more can be expected to respond with relatively rapid height growth. Large numbers of new seedlings can become established at the time of cutting.

Damaging Agents—Black tupelo, particularly where it grows on dry sites, is often affected by fire. Hot fires can cause serious mortality and cull. Fire scars often serve as entry courts for large numbers of heart rot fungi. Ten of 25 black tupelo samples in a study of the central hardwood region had heart rot *(1)*.

The tupelo leafminer *(Antispila nysaefoliella)* and the forest tent caterpillar *(Malacosoma disstria)* attack the tupelos.

Special Uses

Because of its wide range, frequency of occurrence, and the palatability of its fruit and sprouts, black tupelo is an important wildlife species *(4)*. The fruit, high in crude fat, fiber, phosphorus, and calcium, are eaten by many birds and animals. Young sprouts are relished by white-tailed deer but lose palatability with age. Because it is a prolific producer of cavities, black tupelo is usually ranked as one of the more dependable den tree species. Black tupelo is a good honey tree and is often planted as an ornamental.

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SWAMP TUPELO

Swamp tupelo (*Nyssa sylvatica* var. *biflora*) is also called blackgum; another common name is swamp blackgum.

Habitat

Native Range

Swamp tupelo (fig. 3) grows chiefly in the Coastal Plains from Delaware, eastern Maryland, and southeastern Virginia, south to southern Florida and west to eastern Texas. Its range extends north up the

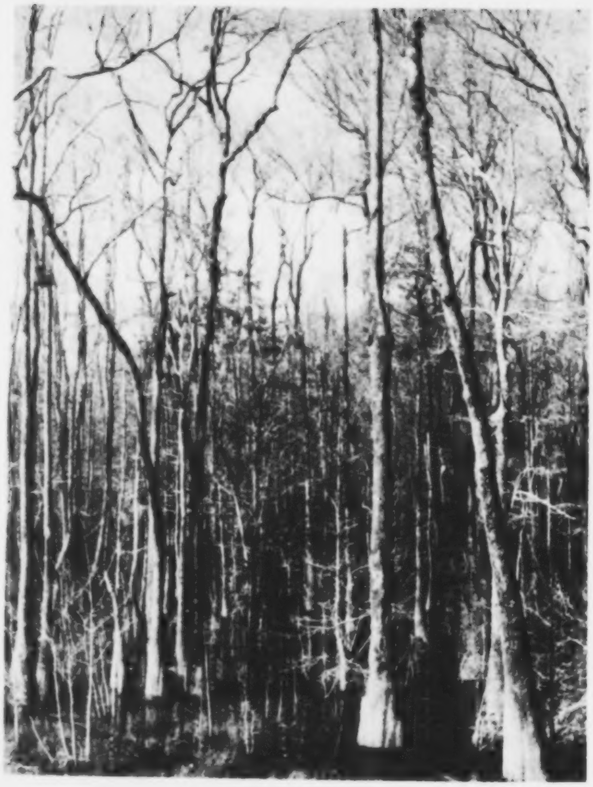

Figure 3—*A swamp tupelo in the lower Coastal Plain of South Carolina.*

Mississippi Valley to southern Arkansas and west and south Tennessee *(17)*.

Climate

Swamp tupelo grows in a warm humid climate. Summers are long and hot; winters are short and mild. The frost-free period ranges from 7 months in the northern area to 11 months in the South. Average July temperature is 26° C (78° F). The average January temperature varies from 2° C (35° F) in the North to 18° C (65° F) in the South. Average annual precipitation varies from 1020 to 1650 mm (40 to 65 in) and is lowest at the northern and western edges of the range.

In the Atlantic Coastal Plain, summer usually is wettest and autumn driest. Precipitation is more uniformly distributed along the gulf coast. Periodic summer droughts occur in the western portion of its range.

Soils and Topography

Swamp tupelo grows on a variety of wet bottomland soils including organic mucks, heavy clays, and wet sands. It occurs mainly on soils in the orders Ultisols, Inceptisols, and Entisols.

Swamp tupelo not only tolerates flooding but actually thrives under those conditions *(16)*. It is seldom found on sites that are not inundated much of the growing season. Swamp tupelo grows in headwater swamps, strands, ponds, river bottoms, bays, estuaries, and low coves. Normally it does not grow in the deeper parts of swamps or overflow river bottoms.

The type of water regime is more important to growth of swamp tupelo than the soil type *(11)*. Best growth is achieved on sites where the soil is continuously saturated with very shallow moving water. Growth can be reduced as much as 50 percent when the water is stagnant, as in ponds. Intermittent flooding, with periodic drying cycles, or continuous deep flooding even by moving water, also reduces growth.

Associated Forest Cover

Swamp tupelo is a major component of the forest cover types Baldcypress–Tupelo (Society of American Foresters Type 102), Water Tupelo–Swamp Tupelo (Type 103), and Sweetbay–Swamp Tupelo–Redbay (Type 104) *(9)*. In the following cover types it is a minor component: Cabbage Palmetto (Type 74), Loblolly Pine–Hardwood (Type 82), Slash Pine (Type 84), Slash Pine–Hardwood (Type 85), Atlantic White-Cedar (Type 97), Pond Pine (Type 98), Pondcypress (Type 100), and Baldcypress (Type 101).

Other trees and shrubs commonly associated with swamp tupelo are red maple *(Acer rubrum)*, buttonbush *(Cephalanthus occidentalis)*, buckwheat-tree *(Cliftonia monophylla)*, dogwood *(Cornus* spp.), swamp cyrilla *(Cyrilla racemiflora)*, swamp-privet *(Forestiera acuminata)*, Carolina ash *(Fraxinus caroliniana)*, loblolly-bay *(Gordonia lasianthus)*, dahoon *(Ilex cassine)*, inkberry *(I. glabra)*, yaupon *(I. vomitoria)*, fetterbush lyonia *(Lyonia lucida)*, and bayberry *(Myrica* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—The minute greenish-white flowers appear in the spring with the leaves, usually in late April in South Carolina. Flowers are polygamo-dioecious, or swamp tupelo may bear staminate and pistillate flowers on separate trees *(22)*. Insects, primarily bees, are the major pollinating vector, but pollen is also spread by wind. The fruit, a drupe, changes from green to a dark blue as it ripens, usually in early November in South Carolina.

Seed Production and Dissemination—Most years swamp tupelo is a prolific seed producer. Over a 4-year period in a 90-year-old stand in South Carolina seed production was as follows:

Year	Seeds/ha	Seeds/acre
1963	135,900	55,000
1964	0	0
1965	1,697,600	687,000
1966	2,058,400	833,000
Average	972,970	393,750

Seed viability, which averaged 60 percent, increased as the season progressed. The seed crop failure in 1964 was probably the result of a late frost.

In South Carolina seedfall begins in early September *(6)*. About 50 percent of the seeds are shed from late October through November. By early December, seedfall is 90 to 95 percent complete. Dissemination is fairly uniform over an entire area. The principal dissemination agents are gravity and birds, mostly robins. The birds consume the fleshy fruits and the seeds are passed through the digestive tract. In southern Carolina, the arrival of large flocks of migratory robins often coincides with peak ripening. Under these conditions birds can disseminate about 55 percent of the total seed crop. These seeds are evenly distributed and have an average viability of 44 percent. Unlike those of water tupelo, fruits of swamp tupelo do not float.

Seedling Development—The seeds normally overwinter and germinate the following spring. Germination is epigeal *(22)*. It does not take place under water, but submerged seeds germinate once the water subsides below the soil surface *(7)*. Germination is rapid in moist, drained conditions at 21° C (70° F) and higher. After germination, seedlings must grow rapidly to keep the apex and leaves above water, because prolonged submergence during active growth will kill them. Submergence during the dormant season, however, has no adverse effect.

Swamp tupelo types are stable and usually regenerate following harvest, although species such as willow (*Salix* spp.) may temporarily dominate some cutover sites *(21)*. Initial seedling establishment is related to seed production, but variation in water table is more important in most years. Environmental conditions under an overstory of 75 to 620 trees per hectare (30 to 250/acre) are favorable for germination and early growth *(5)*. Thus, the shelterwood method can be used to establish seedlings. Regeneration can also be accomplished by clearcutting if it is done following a good seedfall or if, as often happens, advanced reproduction is already established.

Vegetative Reproduction—Stump sprouting is very common following logging *(4,12,19)*. Sprouts arise from suppressed buds and are concentrated near the top of the stump. High stumps, the normal condition since trees are usually cut above the butt swell, have many more sprouts than low-cut stumps. Harvesting trees just before the growing season can increase the growth rate of sprouts.

Stump sprouts can produce seed at 2 years of age. Thus, if the seed crop fails or if unfavorable water conditions prevent a good crop of seedlings from becoming established, sprouts can provide a seed source. However, sprout growth is often so rapid and profuse that all competing vegetation, including natural or planted seedlings, is soon overtopped. Whether or not these sprouts develop into good quality stands is not known.

Sapling and Pole Stages to Maturity

Growth and Yield—On good sites swamp tupelo can attain heights of 37 m (120 ft) and diameters exceeding 122 cm (48 in) *(2)*. Average stand d.b.h. at age 85 is 25 cm (10 in) *(1)*. The average height of dominants at different ages is as follows:

Years	Meters	Feet
20	11	36
30	15	50
40	18	59
50	20	65
60	21	70
70	22	73
80	23	76
90	24	78
100	24	80

Pure, even-aged stands produce an average of 9 m^3/ha (1 cord/acre) per year through age 85. Representative normal yields by age and site index are given in table 1.

Rooting Habit—Swamp tupelo normally develops a taproot and has a swollen base to the mean height of the growing season water level. Water roots, which develop under flooded conditions, help support the tree and capture nutrients. These specialized roots tolerate high carbon dioxide concentrations, oxidize

Table 1—Normal yield for swamp tupelo in southeastern Georgia[1]

Stand age	Site index at base age 50 years		
	15.2 m or 50 ft	22.9 m or 75 ft	30.5 m or 100 ft
yr		*m³/ha*	
30	142	209	357
40	198	292	499
50	243	357	611
60	278	408	699
70	306	449	769
80	328	482	826
90	347	510	873
100	363	533	913
yr		*ft³/acre*	
30	2,030	2,980	5,105
40	2,835	4,170	7,135
50	3,470	5,100	8,725
60	3,965	5,830	9,980
70	4,365	6,415	10,980
80	4,690	6,890	11,795
90	4,960	7,290	12,475
100	5,185	7,620	13,045

[1] Merchantable volume for trees 14 cm (5.5 in) and larger in d.b.h.

the rhizosphere, and carry on anaerobic respiration. Thus, they are the key to the species ability to thrive under flooded conditions *(14,15)*.

Reaction to Competition—Swamp tupelo is classed as intolerant of shade and is best suited to even-age management *(18,21)*. Although seedlings become established under an existing stand they do not develop unless released. Swamp tupelo grows well in stands with relatively high basal areas of 39 to 46 m²/ha (170 to 200 ft²/acre). Many harvested sites develop sapling densities far in excess of optimum. Natural thinning in these overstocked stands is quite slow and, although individual trees respond to thinning, difficult access and damage to sites during logging operations, coupled with low returns, makes thinning undesirable.

Damaging Agents—Swamp tupelo sites are normally quite wet, but during extended drought they do dry out. If the peat that accumulates on many of the sites becomes dry enough to burn, severe fires can cause high mortality and cull in the stand *(3)*.

The forest tent caterpillar *(Malacosoma disstria)* defoliates trees, reducing growth. Severe damage can result in dieback and mortality *(23)*. Various wood-boring insects cause significant degrade in swamp tupelo veneer logs. Tupelo lesion caused by *Fusarium solani* develops on the stem, killing the cambium, which causes swelling and roughened bark *(2)*. Although this is seldom lethal it can cause significant degrade in logs. *Fomes* spp., *Polyporus* spp., *Daedalea ambigua*, *Hydnum erinaceum*, *Lentinus tigrinus*, and *Pleurotus ostreatus* fungi all cause heartrot in swamp tupelo.

Swamp tupelo is very susceptible to sapsucker injury and is readily damaged by salt spray. Sulfate-enriched water can cause seedling mortality *(20)*.

Special Uses

The foliage and twigs of swamp tupelo are browsed by deer *(10)*. Birds and small mammals consume the fruit. The flowers are a source of nectar for bees kept by commercial honey producers. Certain locations, such as the Apalachicola River bottoms of west Florida, produce significant quantities of swamp tupelo honey.

Genetics

Tests with seedlings indicate that there are local populations that are adapted to different habitats *(13)*. The three habitats identified were blackwater rivers, headwater swamps, and ponds.

A shrubby form of swamp tupelo found in the panhandle of Florida may be a local race. Some authors *(8)* consider swamp tupelo a separate species *(Nyssa biflora)* rather than a variety of black tupelo *(N. sylvatica* var. *sylvatica)*, while others suggest it is a variety which will hybridize with black tupelo.

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Ostrya virginiana (Mill.) K. Koch Eastern Hophornbeam

Betulaceae Birch family

F. T. Metzger

Eastern hophornbeam *(Ostrya virginiana)*, also called American hophornbeam, hornbeam, leverwood, and "ironwood," is a small, short-lived tree scattered in the understory of hardwood forests. It has a slow to medium growth rate on a great variety of soils and produces an extremely hard wood. The tree is not large enough for commercially important lumber but is used locally. It makes an attractive landscape tree and provides wildlife with a limited amount of seed.

Habitat

Native Range

Eastern hophornbeam (fig. 1) occurs throughout most of the eastern half of the United States. The range extends from Cape Breton and Prince Edward Island west through southern Ontario, northern Michigan, to southeastern Manitoba; south into North Dakota, the Black Hills of South Dakota and northeastern Wyoming, along the Niobrara River Valley and Delta areas. It is also found in the mountains of Mexico, south to El Salvador and Honduras.

Climate

Climatic conditions vary considerably over the range of eastern hophornbeam. In the northwest corner of its range precipitation is 460 mm (18 in) annually, the frost-free season is 100 days, the mean July temperature is 16° C (60° F), and the mean January temperature is -18° C (0° F). Along the gulf coast precipitation is 1630 mm (64 in) annually, the frost-free season is 290 days, the mean July temperature is 29° C (84° F), and the mean January temperature is 13° C (56° F).

Soils and Topography

Eastern hophornbeam grows on a wide variety of soil and physiographic conditions throughout its range. It is found on soils in all of the major orders in the Eastern United States, Spodosols in the North, Alfisols in the North and Central, Mollisols in the Central, Ultisols in the South, and Entisols and Inceptisols throughout.

Along the northernmost portion of its range, eastern hophornbeam is found on dry-mesic to xeric sites, areas with shallow soils, and bedrock outcrops on upper slopes and ridgetops *(31,53)*. Just to the south within Ontario and Quebec, it grows primarily on mesic and dry-mesic sites. In Wisconsin the species is most abundant on mesic sites usually associated with a mid-catena position, but it also occurs on dry-mesic, wet-mesic, and xeric sites *(12)*.

Mesic sites throughout the Appalachians are most favorable *(32,52)*, but the species tolerates a progressively wider range of conditions northward. In the Smokies and southern Cumberland Plateau it is limited to north slopes, protected lower slopes, ravines, and coves. It grows primarily on dry-mesic and mesic valley bottoms and lower slope positions in the highlands of New Jersey but does extend upslope to drier positions. In Massachusetts it is also found in xeric positions on ridgetops as well *(17,43)*.

From the central lowlands southward the species is associated with wet mesic to dry-mesic sites. It is frequently found on xeric sites in northcentral Florida, however *(35)*. Through the Ozark Plateau, Central Lowlands, and the Kentucky–Tennessee Highland Rim best development occurs on well-drained flood plains of the major rivers, ravines, coves, and lower slopes. Progressing upslope it is less abundant, becoming rare in xeric situations, and it is absent from the wettest sites as on lower flood plains, depressions, sink holes, and bogs *(45,47,49)*. In the south the species is most frequent on terraces of minor streams, common on the well-drained terraces and outwash in major bottoms, and occurs in most upland situations *(40,41)*. Originally it was limited to sites not subject to frequent wildfire in the south such as those protected by bodies of water, swamps, or bottom lands, or those that are less prone to fire such as ravines or steep bluffs along streams *(14)*.

At the westernmost extension of the species range in the Black Hills of South Dakota, the tree grows principally in mesic, deciduous streamside communities at lower elevations and to a much lesser extent on dry-mesic but deep-soiled pine sites.

Eastern hophornbeam grows below elevations of 910 m (3,000 ft) in the northern Appalachians but is most often found at 75 to 230 m (250 to 750 ft) in Quebec *(5)*, and at about 460 m (1,500 ft) in New York *(7)*. Its upper elevational limit is 1520 m (5,000 ft) in the southern Appalachians, although it is more common from 850 to 980 m (2,800 to 3,200 ft). The

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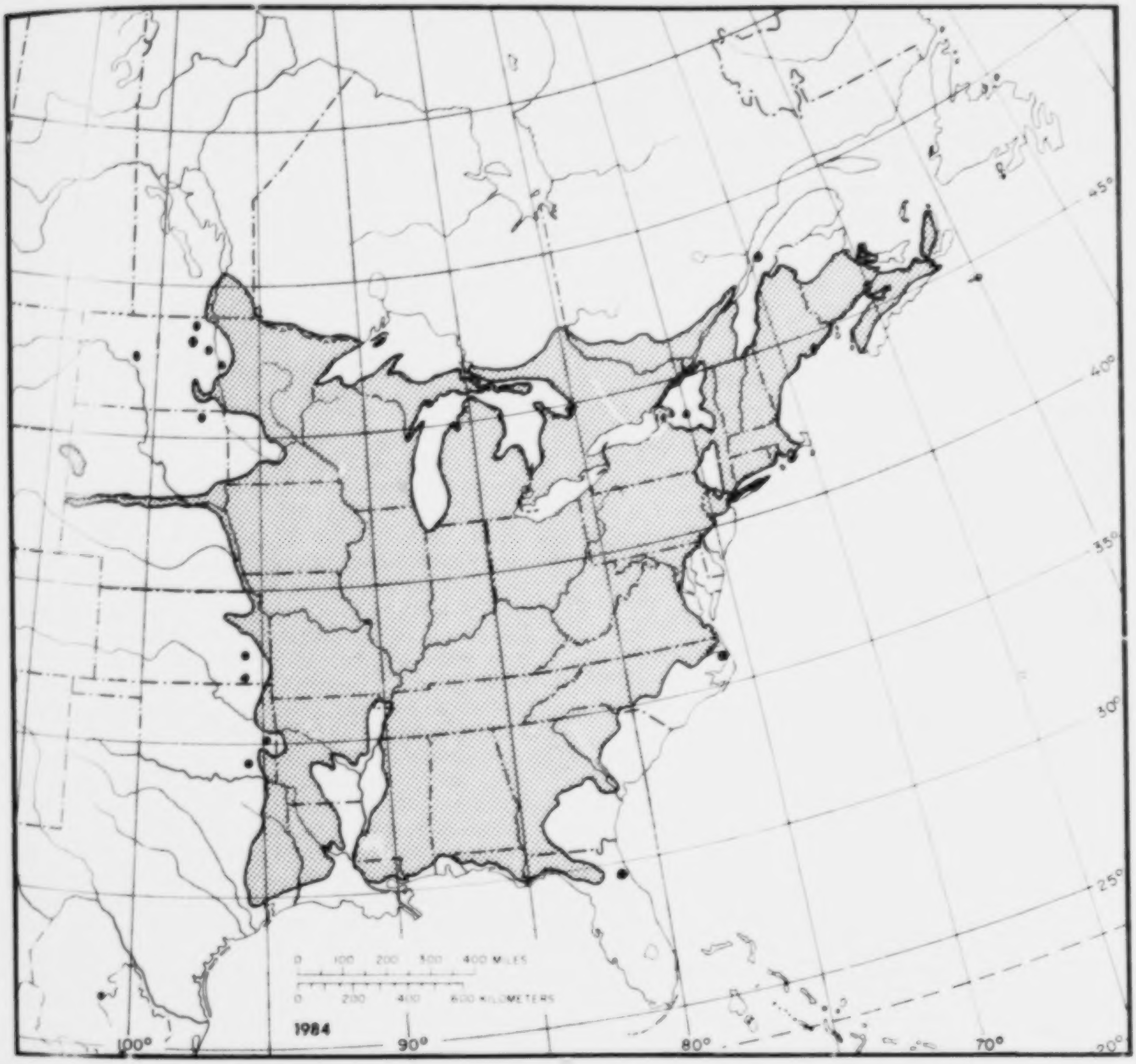

Figure 1—*The native range of eastern hophornbeam.*

lowest slope position it occupies is determined by its intolerance of flooding. It was the third most flood sensitive of 39 species compared in Tennessee, where inundation 16 percent or more of the time killed all eastern hophornbeam *(22)*. Along an Illinois stream it is limited to positions flooded less than 1 percent of the time *(4)*.

Surface soils on sites occupied by eastern hophornbeam include a full range of textures and moisture-drainage classes. Best development of the species is associated with soils that are in loam or loam-modified textural classes and on somewhat poorly drained to well-drained soils. Surface soil pH ranges from 4.2 to 7.6 in the northern half of its range

(10,26). In the mid-South the pH range is narrower—from 4.6 to 5.6 *(8)*. Nevertheless, the species does occur on sites with shallow soils over limestone or soils with limestone fragments at various locations throughout its range.

The calcium content of the foliage of eastern hophornbeam is high in comparison to other species on the same site. Concentrations frequently exceed 2 percent on the basis of ovendry leaf weight *(2,11)*. Nitrogen concentrations range from moderate to high in comparison to the other species on the site, but concentrations of phosphorus and potassium are usually low.

Associated Forest Cover

Eastern hophornbeam is a minor member of most forest communities where it is present. It rarely attains a codominant or dominant crown position in mature stands and is not a commercial species. In the following forest cover types it is only a subordinate species (Society of American Foresters) *(18)*:

Boreal and Northern Forest Region

16	Aspen
20	White Pine–Northern Red Oak–Red Maple
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
26	Sugar Maple–Basswood
27	Sugar Maple
28	Black Cherry–Maple
33	Red Spruce–Balsam Fir
60	Beech–Sugar Maple

Central Forest Region

42	Bur Oak
52	White Oak–Black Oak–Northern Red Oak
55	Northern Red Oak
110	Black Oak

Southern Forest Region *(30)*

82	Loblolly Pine–Hardwood
87	Sweetgum–Yellow-Poplar
91	Swamp Chestnut Oak–Cherrybark Oak

It probably occurs in other types but is omitted from their descriptions, particularly in the South where the types are complex.

The species occurs in all nine forest regions Braun recognizes in the eastern deciduous forest formation *(6)*. One plant association based on the species, in which eastern hophornbeam is second in importance to sugar maple, is recognized in Quebec as the *Ostryo-Aceratum saccaharai* association that occurs on dry knoll tops *(31)*.

From the northern part of its range to Missouri, Tennessee, and Maryland, eastern hophornbeam reaches its greatest abundance in hardwood communities dominated by sugar maple *(Acer saccharum)*, American beech *(Fagus grandifolia)*, or both. It may be the second most important species in some stands. Occasionally, it is abundant in stands dominated by eastern hemlock *(Tsuga canadensis)* and northern red oak *(Quercus rubra)*. In aspen stands, it is a member of a northern hardwood understory reclaiming the site. In the central United States the species is frequently an important subcanopy component of stands dominated by white oak *(Quercus alba)*, black oak *(Q. velutina)*, northern red oak, scarlet oak *(Q. coccinea)*, and southern red oak *(Q. falcata)*.

The species named in the northern forest types plus white ash *(Fraxinus americana)* and American elm *(Ulmus americana)* are eastern hophornbeam's most frequent associates in the North. Progressing southward, the following species are added as associates: bitternut *(Carya cordiformis)*, shagbark *(C. ovata)*, and pignut *(C. glabra)*, hickories; sweetgum *(Liquidambar styraciflua)*; blackgum *(Nyssa sylvatica)*; yellow-poplar *(Liriodendron tulipifera)*; slippery elm *(Ulmus rubra)*; sassafras *(Sassafras albidum)*; and flowering dogwood *(Cornus florida)*.

The extremely species-rich mixed mesophytic forests of the Cumberland Mountains and plateau have minor amounts of eastern hophornbeam.

Within the Piedmont and Coastal Plains of the South the species grows in the southern mixed hardwood and in loblolly *(Pinus taeda)* and shortleaf *(P. echinata)* pine-dominated forests. Although typically a minor component of southern mixed hardwood stands, it is occasionally the second most abundant species *(35,36)*. In these forests it is associated with many trees including American beech, southern magnolia *(Magnolia grandiflora)*, white oak, loblolly pine, and shortleaf pine; and with many understory species including flowering dogwood, American holly *(Ilex opaca)*, American hornbeam *(Carpinus caroliniana)*, tree sparkleberry *(Vaccinium arboreum)*, eastern redbud *(Cercis canadensis)*, and pawpaw *(Asimina triloba)*. Other associated trees include blackgum; sweetgum; yellow-poplar; southern red laurel *(Quercus laurifolia)*, water *(Q. nigra)*, swamp chestnut *(Q. michauxii)*, post *(Q. stellata)*, black, cherrybark *(Q. falcata* var. *pagodifolia)*, shumard *(Q. shumardii)*, and scarlet oaks; mockernut *(Carya tomentosa)*, sand *(C. pallida)*, pignut and bitternut hickories; American basswood *(Tilia americana)*; red *(Acer rubrum)* and Florida *(A. barbatum)* maples; winged *(Ulmus alata)* and slippery elms; and white and green *(Fraxinus pennsylvanica)* ashes.

Shrubs that occur with eastern hophornbeam in the north include mountain maple *(Acer spicatum)*, roundleaf dogwood *(Cornus rugosa)*, American hazel *(Corylus americana)*, beaked hazel *(Corylus cornuta)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, Atlantic leatherwood *(Dirca palustris)*, witch-hazel *(Hamamelis virginiana)*, fly honeysuckle *(Lonicera canadensis)*, American elder *(Sambucus canadensis)*, redberry elder *(Sambucus pubens)*, American yew *(Taxus canadensis)*, mapleleaf viburnum *(Viburnum acerifolium)*, and hobblebush *(Viburnum alnifolium)*. In the South its associated shrub species include devils-walkingstick *(Aralia spinosa)*, St. Andrews cross *(Ascyrum hypericoides)*, smallflower pawpaw *(Asimina parviflora)*, beautyberry *(Callicarpa americana)*, fringetree *(Chionanthus virginicus)*, strawberry-bush *(Euonymus americanus)*, oakleaf hydrangea *(Hydrangea quercifolia)*, southern bayberry *(Myrica cerifera)*, woolly azalea *(Rhododendron viscosum tomentosum)*, greenbriers *(Smilax* spp.), sweetleaf *(Symplocus tinctoria)*, and *Vaccinium* spp.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Eastern hophornbeam is monoecious; from 1 to 3 staminate catkins develop at the end of branches late in the summer that precede pistillate flower development. Pollen forms, matures, and is shed in spring. It is wind disseminated. Solitary pistillate catkins first appear with the beginning of leaf development, and full bloom occurs about a month later. In the southeast, flowering occurs between March 25 and April 16, and in the north, between mid-May and mid-June *(21)*.

Seed Production and Dissemination—The fruits complete development during the summer and are ripe by the end of August in Michigan and as late as October in the South. The hoplike strobile begins to break up immediately after ripening and the seeds are dispersed throughout the fall and into early winter. Seeds should be collected when the strobiles are a pale greenish brown and before they dry enough to shatter. Seeds are light—about 66,000 cleaned seeds per kilogram (30,000/lb). The nuts are 7 mm (0.3 in) long and are enclosed in an inflated sac about 20 mm (0.8 in) long that provides buoyancy and improved dispersal by the wind. Birds provide a secondary means of seed dispersal. Trees begin to be fruitful at age 25. Seed production in northern hardwood stands has averaged 124,000/ha (50,000/acre) *(19,21,37)*.

Seedling Development—Seeds usually germinate in the spring the year after they are shed. Germination is epigeal. The seeds have a form of internal dormancy that requires stratification to overcome. Potential germination is 85 to 90 percent but germination capacity is only 27 to 65 percent *(44)*.

Information is scarce on the relation of germination and seedling establishment to the environment. The occurrence of reproduction on a variety of sites in undisturbed forests indicates its ability to become established on various seedbeds, soils, and moisture regimes under dense shade. Conversely, the ecesis of the species into old fields demonstrates its ability to become established in the open in competition with a heavy cover of grasses and forbs. Mechanical scarification to expose mineral soil seedbeds in an Ontario partially cut sugar maple stand had no effect on eastern hophornbeam abundance after 10 years *(50)*.

Seedlings have the potential for unusually fast juvenile height growth *(27,48,54)*. In Pennsylvania eastern hophornbeam was 2.1 m (7 ft) tall 5 years after a partial harvest of the overstory. In Michigan, the species averaged 3.4 m (11 ft) tall 10 years after an improvement cut and 5.9 m (19.5 ft) tall 20 years after the cut.

Advance reproduction of eastern hophornbeam is aggressive when released by overstory cutting, a trait that makes its proportion in the reproduced stand similar to that in the original stand regardless of the cutting method *(53)*. Its position in the new stand may even be improved if new reproduction of eastern hophornbeam becomes established, as is likely, or if mortality increases among the other species. Increases have occurred after clearcutting and seed-tree and selection cuttings in West Virginia Appalachian hardwood stands on better sites *(48)*. Similarly, the species proportion of the basal area stocking in northern hardwood stands in Wisconsin increased after strip clearcutting and after a shelterwood removal *(21)*. Greater increases in the species relative abundance have occurred when northern hardwood stands less than 40 years old are clearcut because little advance reproduction of other species is present at this time *(28)*.

The species' response to fire apparently is related to the severity of the fire. Areas burned severely enough to kill almost the entire overstory in 21 white oak-scarlet oak stands in Rhode Island contained no eastern hophornbeam 5 to 51 years later. In unburned stands the species made up 10 percent of the understory stems *(9)*. After a prescribed burn of a clearcut aspen stand, eastern hophornbeam remained constant, because new sprouting equalled mortality during the 5 years following the burn *(39)*. Accidental fires in two sugar maple stands in New

York resulted in increased sugar maple and eastern hophornbeam stocking because of sprouting *(46)*. The initial incidence of fire in the Big Woods of Minnesota converted the forest to a thicket of basswood and eastern hophornbeam *(13)*. Subsequent fires converted them to a bur oak savanna.

Vegetative Reproduction—Stump sprouting is common on cut, burned, or injured trees. The proportion of stumps sprouting increases with stump height. Only 17 percent of the stumps cut at ground line sprouted, whereas 40 percent of stumps cut at a height of 15 cm (6 in) sprouted and between 80 and 90 percent of stumps cut at a height of more than 30 cm (12 in) sprouted *(15)*. Sprouts arose from dormant adventitious buds on the stump and no root suckering occurred.

After fires, 62 percent of the top-killed stems in New York *(46)* and 100 percent of those in Minnesota sprouted *(39)*. Number of sprouts per clump averaged 4.4 in New York and 32 in Minnesota. Height growth of the Minnesota sprouts averaged 2.4 m (7.9 ft) after 5 years, which is about average for the other species measured. Height growth of eastern hophornbeam sprouts in an Allegheny hardwood stand exceeded that of other sprouting species *(27)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Eastern hophornbeam trees are normally less than 30 cm (12 in) in d.b.h. and less than 12 m (40 ft) tall, except in east Texas and south Arkansas where they may reach a height of from 15 to 18 m (50 to 60 ft). Occasionally they reach saw log size. The largest tree is 91 cm (36 in) in d.b.h., 22 m (73 ft) tall, and has a crown spread of 27 m (88 ft). It was found in 1976 in Michigan.

The slow growth and small size of the species earn it the title "weed" throughout its range, especially in some areas in the South where it is considered the number one weed species. Eastern hophornbeam usually is discriminated against in stands managed for timber. Silviculturally, more interest has been given to eradicating it than to improving its growth.

Girdling is effective in eradicating the species, killing the tree within 2 years. Herbicides (especially 2,4,5-T, and Tordon 101) applied by mist blowing, tree injection, or spraying at the tree base, on cut stumps, or in frills have also been successful.

Diameter growth rates under individual tree selection management of northern hardwoods in Wisconsin and Michigan average 12 to 13 mm (0.48 to 0.51 in) per decade for poles and saplings, respectively *(21)*. Sugar maple, the most abundant species in these stands, averages from 3.8 to 5.0 cm (1.5 to 2.0 in) per decade for poles and saw logs. Annual ingrowth in these stands is averaging 0.2 and 3.1 trees per hectare (0.1 and 1.3/acre) into the pole and sapling classes, respectively, and exceeds mortality in all but one stand, so stocking of eastern hophornbeam is increasing. Subcanopy trees in Michigan stands average 9.9 m (32.5 ft) tall after 50 years with growth progressively declining as the trees age, the peak growth of 3.3 m (10.8 ft) occurring the first decade *(54)*.

The biomass of trees with basal diameters ranging between 5 and 23 mm (0.2 and 0.9 in) can be estimated by the equation

$$Y = 34.3X \pm \text{[illegible]}$$

where Y is the total plant weight in grams and X is the basal diameter in centimeters; the equation accounts for 98 percent of the variation in weight *(16)*.

Rooting Habit—No information available.

Reaction to Competition—The species typically grows in climax forests in the northern part of its range. It is classed as shade tolerant and reproduces well under full shade. Ecologists rank it high in their ratings of species climax potential *(12,51)*.

In the South the composition of the climax forests has not been clearly identified. The species is associated with later seral stages that follow the pioneer pine communities. Eastern hophornbeam first appears in piedmont pine stands after they are about 90 years old and in bottom-land hardwoods after they are about 36 years old *(38)*. Repeated harvesting of the larger, commercial species from hardwood stands that contain well-developed subcanopies of eastern hophornbeam and its allies may allow the subcanopy to dominate and prevent the reproduction of the original overstory species *(14,29)*.

Damaging Agents—The most important disease problems are the trunk and butt rots. The species is one of the most defective in Ontario—defect claims 20 percent of the gross merchantable cubic foot volumes of trees more than 10 cm (4 in) d.b.h. *(3)*. Losses are greatest in trees 95 to 140 years old and more than 18 cm (7 in) d.b.h., with cull averaging 32 percent. Brown stains cause 62 percent of the defect, while yellow-brown stringy rot, white spongy rot, and an incipient yellow rot account for most of the remaining defect. The organisms primarily responsible are *Stereum murrayi, Phellinus igniarius*, and *Pholiota limonella (3)*.

Throughout its range, eastern hophornbeam is browsed by white-tailed deer only incidentally. Selective deer browsing of more desirable species of reproduction increases the proportion of beech and eastern hophornbeam, which are avoided in heavily browsed regenerated stands in New York (*42*). Beaver in Ohio prefer the species as food—it was the most utilized food after alder and aspen in one drainage (*25*).

Eastern hophornbeam is considered to be relatively free of insect and other disease problems. The species is not readily injured by cold temperatures; succulent growth was not damaged until temperatures dropped below -8° C (17° F) in Wisconsin (*1*). It is sensitive to pollutants in the upper Ohio River Valley, where it does not grow in areas with high exposure to oxides of sulfur or nitrogen, or to chlorine or fluorine (*33*). Its tough, resilient branches resist wind, snow, and ice damage.

Special Uses

Buds and catkins of eastern hophornbeam are important winter food for ruffed grouse, equal to the value of aspen and birch, and the nuts are secondary food in the fall. It is a preferred food for sharp-tailed grouse and wild turkey and is eaten to a lesser extent by bobwhite, red and grey squirrels, cottontails, white-tailed deer, ring-necked pheasant, purple finch, rose-breasted grosbeak, and downy woodpeckers (*23,24*).

The tree is not commonly used as an ornamental because of its slow growth and sensitivity to pollutants.

Genetics

One variety of the species, var. *lasia*, replaces the typical *Ostrya* in the southern half of the species' range. The forma *glandulosa* occurs in the range of the typical *Ostrya* (*20*). The three are distinguished by surface features on new twigs: var. *lasia* is pubescent, forma *glandulosa* is glandular hairy, and the typical plant is glabrous or sparsely pilose. The species has eight pairs of chromosomes.

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Oxydendrum arboreum (L.) DC. Sourwood

Ericaceae Heath family

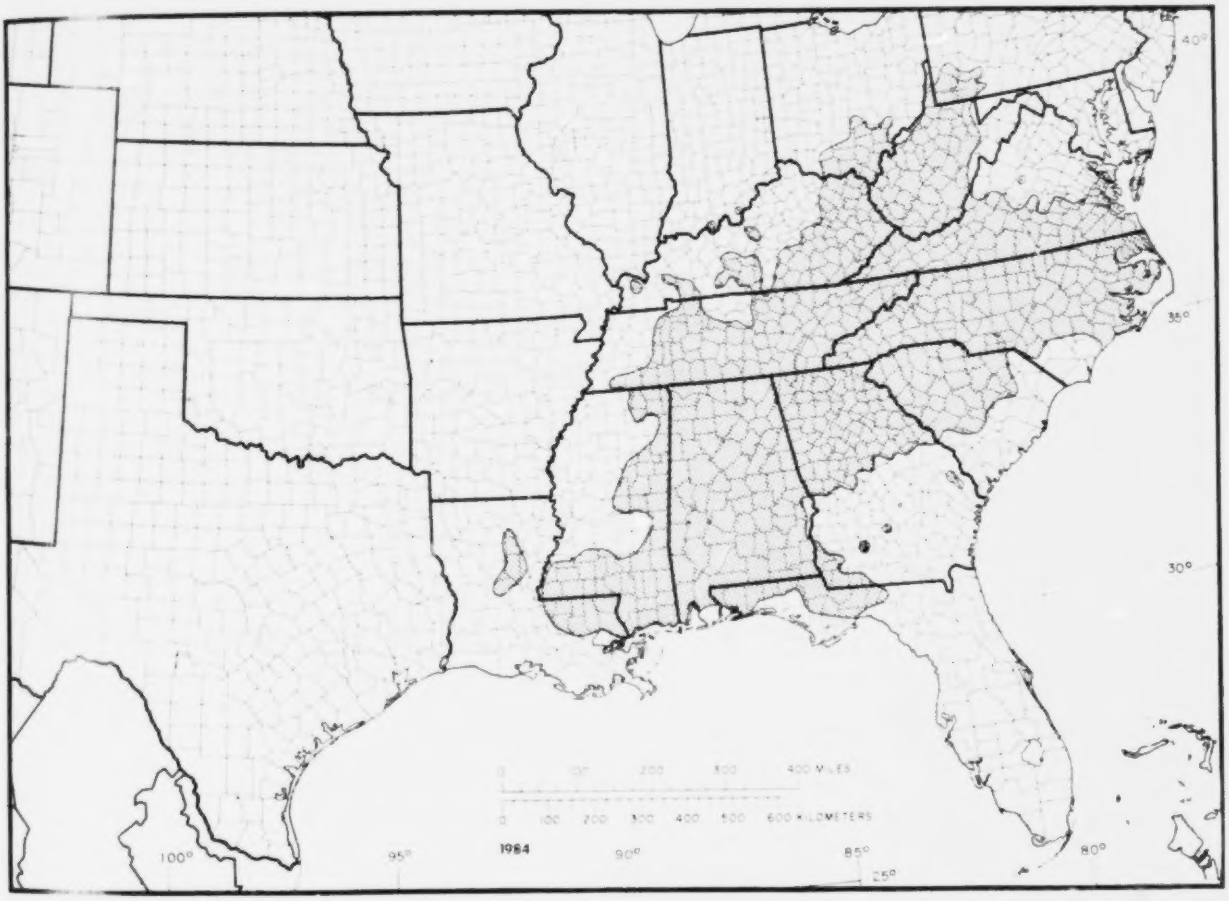
Ronald P. Overton

Sourwood (*Oxydendrum arboreum*) grows in the upland forests of the southeastern United States. Also known as sorrel-tree or lily-of-the-valley-tree, its flowers are an important source of honey in some areas but it is of little value as a timber species. Sourwood sprouts often interfere with the establishment of more desirable species in second-growth and cutover areas. This mid-summer flowering tree is an attractive ornamental.

Habitat

Native Range

Sourwood (figs. 1, 2) is found from southwest Pennsylvania to southern Ohio, and southern Indiana,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35°
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25°
100°
95°
90°
85°
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1984

Figure 1.—*The native range of sourwood.*

The author is Geneticist, Northeastern Area, State and Private Forestry, Radnor, PA.

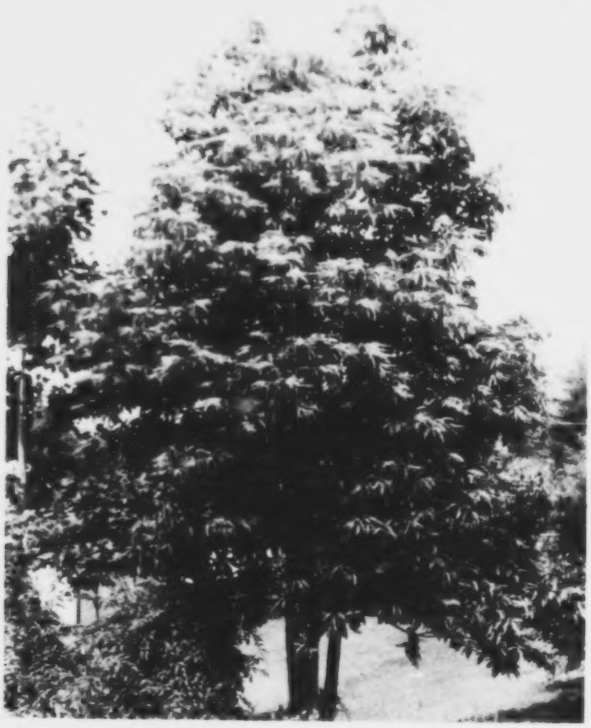

Figure 2—*Sourwood flowers in midsummer and makes an attractive lawn tree.*

south to southeastern Louisiana and the coastal region of Mississippi, Alabama, and northwest Florida; west to western Kentucky and Tennessee, and to the Delta in Mississippi; and east to the Atlantic coast from southern Virginia to central North Carolina, and to the edge of the Coastal Plain in South Carolina and Georgia. The main range lies between latitude 30° and 40° N. and longitude 75° and 92° W. Sourwood reaches its largest size on the western slopes of the Great Smoky Mountains in Tennessee.

Climate

Annual precipitation within the range of sourwood varies from 1020 mm (40 in) in the North to 2030 mm (80 in) in the central Appalachians. Warm season precipitation ranges from 530 mm (21 in) in the North to 910 mm (36 in) on the gulf coast and in the Appalachians, and annual snowfall varies from none along the gulf coast to 152 cm (60 in) in the Appalachians. The length of the growing season fluctuates from 150 days in the mountains of southern Pennsylvania to 300 days in northern Florida. Temperature extremes vary from -29° C (-20° F) to 42° C (107° F) within the range of sourwood.

Soils and Topography

In the central Appalachians sourwood is most abundant on subxeric open slopes and ridges occupied by chestnut oak (*Quercus prinus*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), and Virginia pine (*Pinus virginiana*). It appears less frequently on more mesic sites such as coves and sheltered slopes (*17*). Throughout this area sourwood is found up to 1520 m (5,000 ft) but rarely to 1710 m (5,600 ft) (*13*).

Sourwood grows throughout the Piedmont uplands. It is also found along Piedmont streams on well-drained lowland areas not subject to ordinary flooding (*10*). Where it enters the Coastal Plain it is found on the gently rolling areas of the upper portion; toward the coast it is restricted to old dunes and well-drained slopes and ridges above streams and swamp borders (*4,16*).

Like most of the Ericaceae, sourwood generally does not grow on soils of limestone origin (*8,11*) but is most commonly found growing on soils in the orders Ultisols, Inceptisols, and Entisols.

Associated Forest Cover

Sourwood is an understory to midcanopy associate of the following forest cover types (Society of American Foresters) (*6*):

40	Post Oak–Blackjack Oak
44	Chestnut Oak
51	White Pine–Chestnut Oak
52	White Oak–Black Oak–Northern Red Oak
53	White Oak
75	Shortleaf Pine
76	Shortleaf Pine–Oak
78	Virginia Pine–Oak
79	Virginia Pine
81	Loblolly Pine
82	Loblolly Pine–Hardwood
110	Black Oak

Other associates, in addition to the cover type species, are sweetgum (*Liquidambar styraciflua*); yellow-poplar (*Liriodendron tulipifera*); scarlet and southern red oak (*Q. falcata*); red and sugar maple (*Acer rubrum* and *A. saccharum*); shagbark, bitternut, pignut, and mockernut hickory (*Carya ovata, C. cordiformis, C. glabra,* and *C. tomentosa*); white ash (*Fraxinus americana*); American beech (*Fagus grandifolia*); eastern hemlock (*Tsuga canadensis*); flowering dogwood (*Cornus florida*); sassafras (*Sassafras albidum*); American hornbeam (*Carpinus caroliniana*); eastern hophornbeam (*Ostrya virginiana*); and redbud (*Cercis canadensis*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sourwood is among the latest of the flowering shrubs and trees to bloom. The white, bell-shaped perfect flowers appear from late June to August in copious masses on one-sided racemes clustered in an open panicle. The flowers are insect pollinated and are an important honey source in some areas (*14*).

Seed Production and Dissemination—The fruit is a capsule 6 to 13 mm (0.25 to 0.5 in) in length. It ripens in September and October, and the tiny seeds are dispersed gradually throughout the winter by the dehiscing capsule. The number of seeds in clean lots range from 4 080 000 to 12 125 000 seeds per kilogram (1,850,000 to 5,500,000/lb) (*14*).

Seedling Development—Seedbed requirements are not known for natural regeneration. In the Piedmont, however, sourwood seedlings and saplings are found in all stages of succession from young pine stands to the oak-hickory climax (*10*). This indicates that seed germination and establishment may occur on litter and under partially shaded conditions.

Techniques have been described for sourwood seed collection, storage, and germination (*2,5,14*). Acid sandy peat is recommended as a seedbed for sourwood. Germination is epigeal.

Vegetative Reproduction—Sourwood sprouts prolifically and persistently from the stump and often must be treated with herbicides to release more desirable species in second growth and in cutover areas (*7,9,12,15*). Sourwood is difficult to propagate from cuttings. A single report found softwood cuttings (short side shoots), made with a heel and taken in late July with a 90 ppm IBA soak, rooted 80 percent when placed in a sand:peat (equal volumes) mix under mist (*5*). No reports were found of propagation by grafting.

Sapling and Pole Stages to Maturity

Growth and Yield—The maximum size for sourwood is 24 m (80 ft) in height and 61 cm (24 in) in diameter. It is typically much smaller, reaching 6 to 15 m (20 to 50 ft) in height and 20 to 30 cm (8 to 12 in) in diameter (*11*).

Sourwood usually remains in the forest understory from seedling to maturity. It occasionally enters the overstory in Piedmont lowland pine stands, but on upland sites it attains the upper canopy only if some disturbance removes the overtopping vegetation (*10*).

Sourwood develops a slender trunk and small crown in dense stands. In more open situations it forms a short, often leaning trunk dividing into several stout, ascending limbs. Growth is slow in established stands, but the initial growth of sprouts in cutover areas is rapid enough to hinder establishment of more desirable species (*7,12*). Per-acre volume estimates are not available for this species because it usually grows in mixture with other species rather than in pure stands.

Rooting Habit—No information is currently available on the rooting habit of sourwood.

Reaction to Competition—Sourwood is classed as tolerant of shade and can grow and reproduce in the understory of climax (oak-hickory) forests (*3,10,11*). Its response to release is not definitely known but is thought to be poor.

Damaging Agents—Several insects attack sourwood but normally do no serious harm (*1*). The dogwood-twig borer, *Oberea tripunctata*, and the twig girdler, *Oncideres cingulata*, attack the twigs; the fall webworm, *Hyphantria cunea* (*7*), and the hickory horned devil (the larva of the regal moth), *Citheronia regalis*, attack the foliage.

There are no known reports of serious diseases that affect sourwood.

Special Uses

Sourwood is occasionally used as an ornamental because of its brilliant fall color and midsummer flowers (*7*). It is of little value as a timber species; the wood is heavy and is used locally for handles and fuel and in mixture with other species for pulp (*8*). Sourwood is important as a source of honey in some areas and sourwood honey is marketed locally.

Genetics

No studies on the genetic characteristics of sourwood have been reported.

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Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud.
Royal Paulownia

Scrophulariaceae Figwort family

F. T. Bonner

Royal paulownia *(Paulownia tomentosa)* is an introduced ornamental that has become well established in this country. It is also known as princess-tree, empress-tree, or paulownia. Aside from its continuing ornamental use, the species has value for its small saw logs that are in demand for specialty products. Its capacity to "pioneer" disturbed exposed sites has made royal paulownia a favorite for strip-mine spoilbank reclamation.

Habitat

Native Range and Climate

Royal paulownia is a native of eastern Asia. It has been widely planted in North America from Montreal to Florida and west to Missouri and Texas. It has also been planted in some Pacific States. The tree is moderately cold hardy and has naturalized principally in the East and South. In China, the natural range is south of the 0° C (32° F) January isotherm in areas which receive an annual rainfall of at least 1020 mm (40 in) *(5)*.

Soils, Topography, and Associated Forest Cover

Naturally seeded or planted royal paulownia survives and grows best on moist, well-drained soils of steep slopes or open valleys *(3,7)*, but it will germinate and grow on almost any moist, bare soil. A highly adaptable "escapee" such as royal paulownia is found in many site, soil, and forest type conditions, including soils commonly found in the order Alfisols.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The perfect flowers of royal paulownia are borne in terminal panicles up to 25 cm (10 in) long in April and May. They are violet or blue and their appearance before the leaves emerge is quite striking. The fruits are ovoid, pointed woody capsules about 30 to 45 mm (1.25 to 1.75 in) long (fig. 1). They turn brown as they mature in September or October and persist on the tree through the winter *(1)*.

Seed Production and Dissemination—Royal paulownia trees start bearing seed after 8 to 10 years and are very prolific *(2)*. Each capsule contains up to 2,000 seeds, and a large tree may produce as many as 20 million seeds a year. The tiny, flat, winged seeds weigh about 0.17 mg (170,000 seeds/oz). As the capsules break open on the trees throughout the winter and into spring, wind dissemination occurs easily *(1)*.

Seedling Development—The seeds of this species germinate quickly and grow rapidly when conditions are favorable. The seeds are not dormant, but laboratory studies have found that light is required for germination *(1)*. Cold storage reduces the light requirement, however *(7)*. Germination is epigeal. Like most pioneer species, *P. tomentosa*

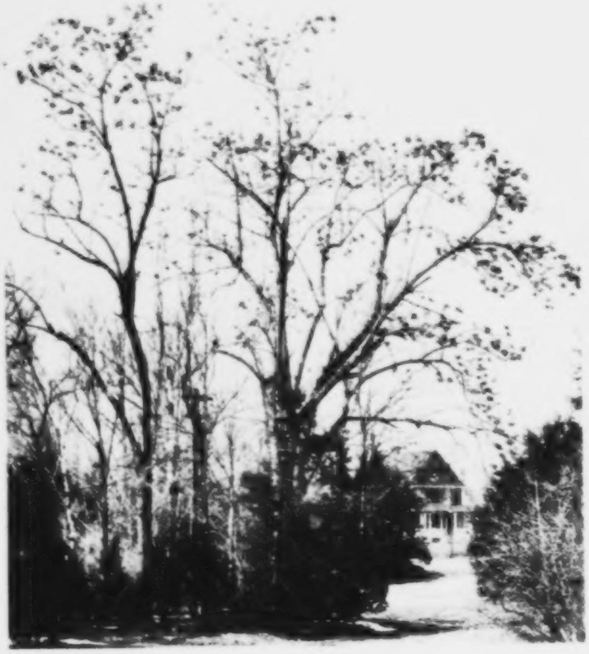

Figure 1—*Planted paulownia trees with persistent woody seed capsules in winter.*

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needs bare soil, sufficient moisture, and direct sunlight for good seedling establishment. Seedlings are very intolerant of shade.

Vegetative Reproduction—Royal paulownia roots sprout easily. In fact, lateral root cuttings of 1-year-old seedlings can be used for propagation directly in the field *(7)*.

Sapling and Pole Stages to Maturity

Growth and Yield—On good sites royal paulownia grows rapidly. Plantation spacings of 1.2 by 1.2 or 1.8 by 1.8 m (4 by 4 or 6 by 6 ft) have been recommended; saw logs can be expected in 15 years. Heights at maturity range from 9 to 21 m (30 to 70 ft) *(3,7)*. Heights of 13 m (43 ft) in 11 years have been reported in Russia. On poor sites, such as surface mine spoils, growth is considerably slower. The ability of royal paulownia to survive, grow, and reproduce on such harsh, exposed sites, however, has made it a favorite for revegetating surface mine areas. The tree thrives on dry southern aspects, even though it generally has a shallow root system *(7)*.

Rooting Habit—No information available.

Reaction to Competition—Since royal paulownia is a naturalized exotic that is only now being planted, little is known about its silviculture. Like most pioneer species, however, it is classed as intolerant of shade and competing vegetation.

Damaging Agents—No major insect pests are known for royal paulownia in the United States. Minor damage from several foliage diseases has been reported on the species. The most common, *Phyllosticta paulowniae*, produces small brown spots on the leaves, and two powdery mildews, *Phyllactinia guttata* and *Uncinula clintonii*, have also been found *(4)*. No major disease problems have appeared yet in the United States.

Special Uses

Royal paulownia was introduced into this country as an ornamental, and it still retains some popularity for that purpose. Its use in reclamation of the disturbed soils of surface mines grows yearly. The wood is highly prized for the manufacture of specialty items in Asia, and there is a brisk export business of logs to Japan. The export market has led to establishment of commercial plantations in this country.

Genetics

Some authorities list 15 species of paulownia, but only 6 species from China are generally recognized *(7)*. This may indicate considerable natural variation to select from, but there are no published reports of genetic studies in the United States.

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Persea borbonia (L.) Spreng. Redbay

Lauraceae Laurel family

R. H. Brendemuehl

Redbay (*Persea borbonia*), also called shorebay, is an attractive aromatic evergreen tree or shrub of the southeastern Coastal Plains. This tree's size and growth habit varies considerably over its range and commercially important trees are not common. The wood takes a fine polish and is used locally for cabinetwork and boatbuilding. The seeds are eaten by wildlife and deer browse the foliage. The leaves are used as a seasoning for cooking. Redbay is also planted as an ornamental.

Habitat

Native Range

Redbay (fig. 1) is a minor hardwood of southeastern and southern United States. It is a common but seldom an abundant component of the swamp forests of the Atlantic and Gulf Coastal Plains from southern Delaware south through

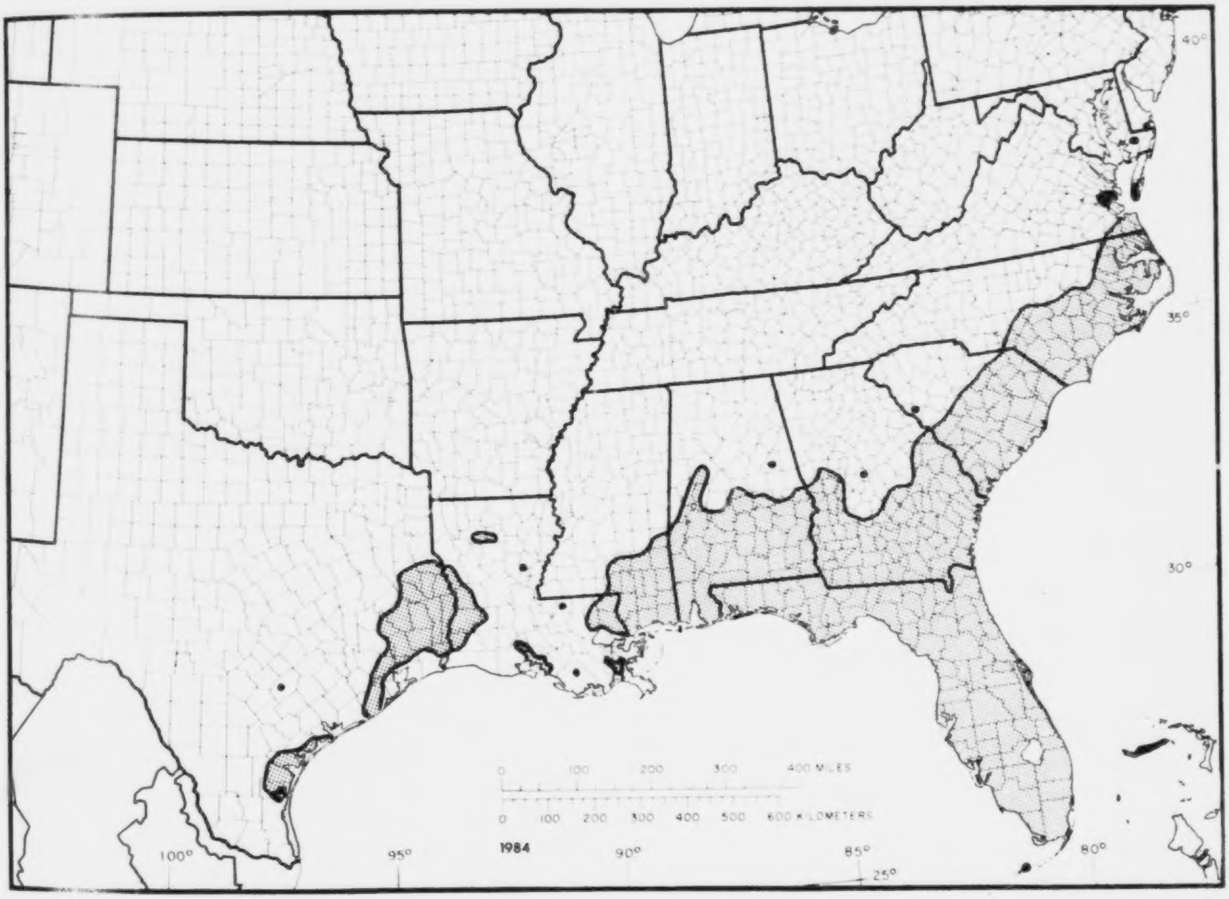

Figure 1—*The native range of redbay.*

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Florida and west to the lower Texas gulf coast *(7)*. It also grows in the Bahamas.

Climate

Redbay grows in a climate ranging from warm-temperate along the Atlantic Coast to semitropical in southern Florida and the lower gulf coast of Texas. The frost-free period varies from a minimum of 200 days to a maximum of 365 days and is more than 250 in much of its range. Average January temperatures of these coastal areas range from 3° C (38° F) in southern Delaware to 20° C (68° F) in south Florida, with 10° to 13° C (50° to 56° F) characteristic of most of this region. Summers are hot and humid. Average July temperatures range from 26° to 28° C (78° to 82° F). Temperatures above 38° C (100° F) or below -12° C (10° F) seldom occur over most of this species range.

Average annual rainfall within the natural range of redbay varies from a low of 1020 mm (40 in) in southern Delaware increasing to about 1320 mm (52 in) along the Atlantic coast of Florida and reaches a maximum of 1630 mm (64 in) in several areas along the gulf coast. Rainfall is quite well distributed, with about 55 percent of the total annual rainfall occurring in the warm season (April through September). Periodic summer droughts are more common in the western part than in the rest of this species range *(9)*.

Soils and Topography

Redbay (fig. 2) is found growing on the borders of swamps and swampy drains in the rich, moist, mucky soil of the lower Coastal Plain. Such muck swamps are not of alluvial origin but generally originate from impoundment of water in land-locked depressions. The water of these swamps is usually dark brown from accumulated organic matter. The bottoms of the swamps do not provide firm support. Sites similar to the deep muck swamps are found in the shallow ponds, strands, and pocosins in the longleaf, slash, and pond pine woods but here tree growth is usually stunted *(8)*. These soils are most commonly found in the order Histosols.

Associated Forest Cover

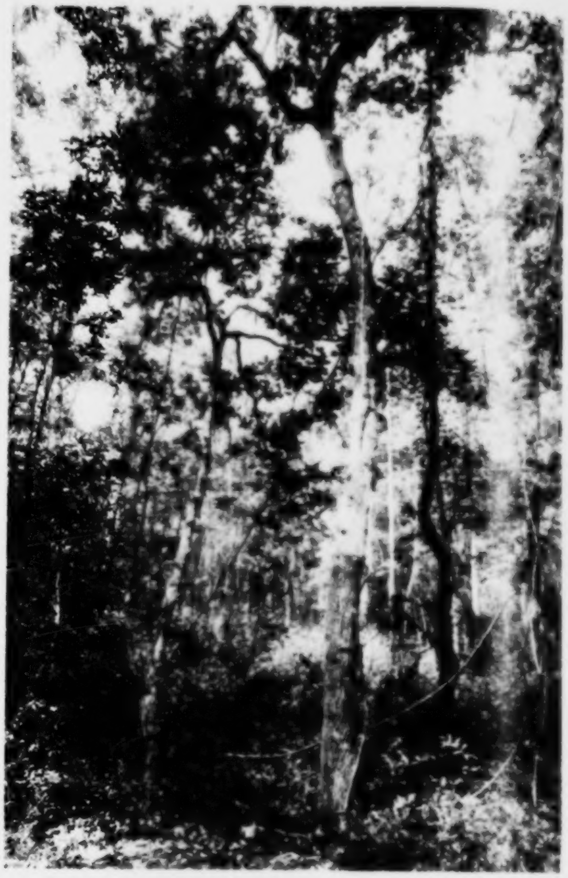

Figure 2—*Two stems of redbay, one overtopping another on the edge of a Dorchester County swamp in South Carolina.*

In the forest cover type Sweetbay–Swamp Tupelo–Redbay (Society of American Foresters Type 104), redbay is a major component *(1)*. Stocking within this type may consist of combinations of any two or all three of these species, but locally a single species may dominate. It is a common associate of the following cover types: Loblolly Pine–Hardwood (Type 82), Pond Pine (Type 98), Baldcypress–Tupelo (Type 102), and Water Tupelo–Swamp Tupelo (Type 103). Redbay is a minor component of the following cover types: Cabbage Palmetto (Type 74), Loblolly Pine (Type 81), Atlantic White-Cedar (Type 97), Pondcypress (Type 100), and Baldcypress (Type 101).

Numerous species that grow on moist to wet sites may be associated with Sweetbay–Swamp Tupelo–Redbay, depending on the geographic location, site, and stand history. Common hardwoods include red maple *(Acer rubrum)*, black tupelo *(Nyssa sylvatica)*, loblolly-bay *(Gordonia lasianthus)*, sweetgum *(Liquidambar styraciflua)*, water oak *(Quercus nigra)*, laurel oak *(Q. laurifolia)*, yellow-poplar *(Liriodendron tulipifera)*, and southern magnolia *(Magnolia grandiflora)*. Associated conifers include slash pine *(Pinus elliottii)*, longleaf pine *(P. palustris)*, loblolly pine *(P. taeda)*, pond pine *(P. serotina)*, baldcypress *(Taxodium distichum)*, pondcypress *(T. distichum* var. *nutans)*, and Atlantic white-cedar *(Chamaecyparis thyoides)*. Small trees and shrubs associated with redbay include buckwheat-tree *(Cliftonia monophylla)*, dahoon *(Ilex cassine)*, yaupon *(I. vomitoria)*, inkberry *(I. glabra)*, lyonia fetterbush *(Lyonia lucida)*, bayberry *(Myrica* spp.), and poison-sumac *(Toxicodendron vernix)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The flowers are perfect, appearing in the spring in the axils of the new foliage. Insects, primarily bees, are the principal pollination vector; however, pollen is also disseminated by wind. The fruit is a small drupe about 13 mm (0.5 in) long that is bright blue or blue-black when ripe. A thin layer of rather dry flesh surrounds the seed or pit of the fruit *(4)*.

Seed Production and Dissemination—Redbay produces annual crops of fruits. Seeds are disseminated mainly by several forms of wildlife, including songbirds, white-tailed deer, bobwhite, wild turkey, and black bear. No direct information is available on size of the seed but based upon drupes of similar size from *Nyssa*, it is estimated that there are approximately 4,630 seeds per kilogram (2,100/lb).

Seedling Development—Germination of redbay seed is hypogeal. No further information on seedling development was available.

Vegetative Reproduction—No information on vegetative reproduction of redbay could be found in the literature.

Sapling and Pole Stages to Maturity

Growth and Yield—Redbay is included in a list of commercial trees of southern hardwood forests, but its growth or the size it attains varies considerably over its range. Presumably these differences in growth are a reflection of variation in site quality *(8)*.

One source *(4)* describes redbay as a beautiful evergreen tree, sometimes 18 to 21 m (60 to 70 ft) in height and 61 to 91 cm (24 to 36 in) in diameter. Under forest growth conditions it develops a clear, cylindrical bole and a dense, pyramidal crown with ascending branches.

A second source *(3)* describes redbay as a small evergreen tree seldom more than 9 to 15 m (30 to 50 ft) tall with a trunk diameter of 31 to 61 cm (12 to 24 in). Redbay found growing in the pocosins along the Atlantic Coast has been described as a shrub.

Rooting Habit—Information pertaining to this aspect of the life history of redbay could not be found in the literature.

Reaction to Competition—Redbay is classed as tolerant of shade but is also found growing well in the open, and in both young and old forest stands. Reproduction is generally erratic and scattered in groups among swamp tupelo and sweetbay. Overstory competition may account for the scarcity and poor form of redbay growing under certain forest conditions *(8)*.

Damaging Agents—Fire may cause substantial damage to redbay. Fire scarring with the associated deterioration of the butt portion of the tree is common. It may also prevent or forestall the establishment of reproduction.

Insects or diseases apparently do not cause serious damage to redbay. It is the principal host of *Trioza magnoliae*, a psyllid or jumping plant louse. This psyllid forms large, unsightly galls on redbay leaves but apparently causes little damage to the tree because a large proportion of the leaves remain unaffected *(6)*. A leaf spot of redbay caused by the fungus *Phyllachora perseae* has been reported. Evidently this disease is not a serious problem because only a portion of the leaf area is affected *(5)*.

Although some species of the genus *Persea* are susceptible to a root disease caused by the fungus *Phytophthora cinnamomi*, redbay is resistant. This resistance is due to a borbonol, a preformed antifungal substance that is a component of the roots and stems of certain species of *Persea*. Some species of this genus, including several avocado cultivars highly susceptible to this root disease, do not contain antifungal compounds with the properties of borbonol *(10)*.

Special Uses

The wood is heavy, hard, strong, and bright red, with a thin, lighter colored sapwood, but it has no established place in commerce. It is used locally for cabinet making and interior finish and for boatbuilding. Dried leaves of redbay make an excellent substitute for those of the tropical bay and may be used in the same way for seasoning food. The tree is occasionally used as an ornamental because of the evergreen leaves and its fruit.

Redbay is reported to be of significant importance to wildlife. The fruit is eaten by several species of songbirds and wild turkey. In order of volumetric importance, the redbay fruits were in 15th place in a list of 63 food items. Redbay seeds may form a sizable portion of the bobwhite diet during the fall and winter months. The fruits and leaves of redbay are eaten by deer. It is browsed heaviest in fall and winter but withstands such grazing well. As much as 40 percent of the annual growth has been removed as browse for 2- or 3-year periods without causing death of the plants. Reports that black bear consume both the fruits and leaves of redbay have been noted in North Carolina and Florida *(2)*.

Genetics

No information on the genetics of redbay is currently available.

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Pithecellobium saman (Jacq.) Benth.   Monkey-Pod

Leguminosae   Legume family

Roger G. Skolmen

Monkey-pod *(Pithecellobium saman)*, samán in Spanish, is a fast-growing tree that has been introduced to many tropical countries throughout the world from its native habitats in Central America and northern South America. Although generally planted as a shade tree and ornamental, it has been naturalized in many countries and is greatly valued in pastures as shade for cattle. Short-boled, with a spreading crown when open grown, it forms a long, relatively straight stem when closely spaced. Its wood is highly valued in some locations for carvings and furniture *(7)*.

The most widely used common name for the species is raintree, from the belief that the tree produces rain at night. The leaflets close up at night or when under heavy cloud cover, allowing rain to pass easily through the crown. This trait may contribute to the frequently observed fact that grass remains green under the trees in times of drought. However, the shading effect of the crown, the addition of nitrogen to the soil by decomposition of litter from this leguminous tree, and possibly, the sticky droppings of cicada insects in the trees all contribute to this phenomenon *(3)*. The Hawaiian common name, monkey-pod, is used here because it is a logical derivation of the scientific name *Pithecellobium* (monkey earring in Greek). Besides monkey-pod, raintree, and saman, which is its name throughout Latin America, the tree is called mimosa in the Philippines.

Habitat

Native Range

Monkey-pod is native from the Yucatan Peninsula in Mexico, through Guatemala to Peru, Bolivia, and Brazil *(3)*. It grows naturally in latitudes from 5° S. to 11° N. *(13)*. Cultivated throughout the tropics as a shade tree, it has been found in Burma, Ceylon, India, Jamaica, Nigeria, Sabah, Trinidad, Uganda, and the island of Zanzibar *(12)*. The species is naturalized in most of these countries as well as in the Philippines and Fiji *(7)*.

In the United States and its possessions, monkey-pod grows in Hawaii, Florida, Puerto Rico, the Virgin Islands, Guam, and the Northern Marianas. It is naturalized in Hawaii, Puerto Rico, and the Virgin Islands *(3,10)*. The tree was reportedly introduced into Hawaii in 1847, when Peter A. Brinsmade, a businessman visiting Europe, returned to Hawaii, presumably via Panama, with two seeds, both of which germinated. One of the seedlings was planted in downtown Honolulu, the other at Koloa on the island of Kauai. These seedlings are possibly the progenitors of all the monkey-pod trees now in Hawaii *(1)*. Monkey-pod may have been introduced into Puerto Rico and Guam as early as the 16th century.

Climate

Monkey-pod grows in a broad annual rainfall range of 640 to 3810 mm (25 to 150 in). On wet sites (1270 mm [50 in] or more), its growth is often rapid. This rapid growth is at times objectionable because the tree forms a large mat of surface roots and the crown becomes top heavy, thereby overbalancing the tree *(5)*. In Hawaii, the climate in locations where the tree is naturalized and spreading rapidly has winter maximum rainfall ranging from 1140 to 2030 mm (45 to 80 in), with a temperature range of 10° to 30° C (50° to 86° F). These climatic conditions are found between elevations of 15 to 245 m (50 to 800 ft) at several sites on three islands. Elsewhere, the tree is reported to grow at elevations of 0 to 700 m (0 to 2,300 ft) *(15)*. It is, however, very intolerant of frost and also, if grown near the shore, of windblown saltwater spray.

Soils and Topography

Monkey-pod attains its best growth on deep alluvial soils that are well drained and neutral to slightly acid in reaction. In Hawaii, most areas to which monkey-pod is well adapted are used for cultivated crops. It has naturalized, however, on gently to steeply sloping Oxisols and Inceptisols on certain sites. On these sites it is most common in gullies where the soil is deeper and more moist than on adjacent hills and ridges. It can, however, grow well on a wide variety of soils when planted and can withstand seasonal flooding *(15)*.

Associated Forest Cover

Monkey-pod is frequently found on old home sites near streams in the forests of Hawaii where it is

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usually associated with mango (*Mangifera indica*), ti (*Cordyline terminalis*), guava (*Psidium guajava*), and other escaped domestic plants. Where naturalized, it is associated primarily with grasses, although occasionally with such trees or shrubs as koa-haole (*Leucaena leucocephala*), Java-plum (*Eugenia cumini*), and Christmas-berry (*Schinus terebinthifolius*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Monkey-pod may flower at any time of the year in Hawaii, but it usually flowers from April to August, with the peak of flowering in May. The flowers are perfect and form in umbels. The clusters, with their numerous pink stamens, 3.8 cm (1.5 in) long, look like powderpuffs in the tree crown. The flowers are insect pollinated. Seed pods develop in from 6 to 8 months and fall to the ground intact, usually between December and April in Hawaii. The dark brown and relatively straight pods are usually 15 to 20 cm (6 to 8 in) long and contain from 5 to 20 seeds *(3,8)*.

Seed Production and Dissemination—Seeds are reddish-brown beans about 13 mm (0.5 in) long that drop from the pods when they open on the ground. Although the seeds are hard coated and long lived, some germinate soon after moistening by soil contact, resulting in a short period of prolific reproduction even under lawn and garden trees. Most or all of the reproduction dies or is destroyed by insects, rodents, and lawn mowing. Seeds are easily collected by gathering pods on the ground and drying them under cover until they open. Natural dissemination is by birds and rodents.

Seeds number from 4,400 to 7,000/kg (2,000 to 3,200/lb) *(15)*. They can be stored dry at 0° to 3° C (32° to 38° F) in closed containers for lengthy periods with little loss of viability. Seeds are normally scarified; they are placed in water at 100° C (212° F), then allowed to cool overnight. Scarified seeds usually germinate 3 to 4 days after sowing.

Seedling Development—Germination is epigeal. Seedlings are usually grown from seed planted in containers. In Hawaii, polyethylene bags are now the most commonly used containers for this purpose. Monkey-pod seedlings have also been grown in seed beds and successfully planted bare-root in Hawaii, but not on a large scale. Severe drought stress usually results in high seedling mortality following bare-root planting. Nursery seedlings are of plantable size in about 4 months *(15)*.

Seedlings grow rapidly if maintained, reaching 2 to 3 m (6 to 10 ft) within 1 year after planting. Natural seedlings, or planted seedlings that are not weeded, are strongly inhibited by competition and grow much more slowly. Seedlings and mature trees are intolerant of shade *(15)* and extremely susceptible to damage by overspray of herbicides used in weed control.

Vegetative Reproduction—Monkey-pod roots easily. Hardwood (leafless) cuttings, ranging in size from 1 by 15 cm (0.4 by 6 in) to stems and branches of mature trees, can be rooted in moist soil on a site without use of mist or shade. In Honolulu, it is common practice to transplant huge trees by cutting away almost all the roots and all the branches. Trees grown at close spacing in the forest frequently have branch-free stems 4 to 5 m (13 to 16 ft) tall and are transplanted to parking lots and parks as "instant" full-size shade trees. Despite the ease with which it can be vegetatively propagated, monkey-pod is almost always started from seed.

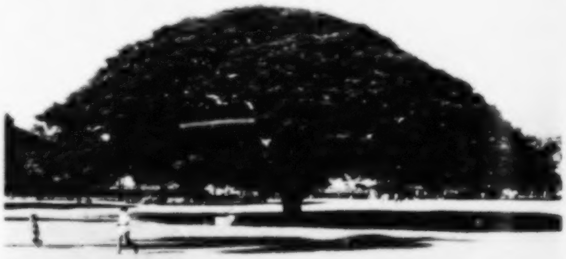

Figure 1—*Monkey-pod shade tree at Moanalua Gardens, Honolulu, showing large, rounded crown, typical of open grown trees of this species.*

Sapling and Pole Stages to Maturity

Growth and Yield—One of the best known trees of this species is in Trinidad. When a little more than 100 years old, this tree had a trunk 244 cm (96 in) in diameter, was (reportedly) 44.8 m (147 ft) tall, and had a crown spread of 57 m (187 ft) *(3)*. The large, rounded crown of open-grown trees (fig. 1) provides shade over a wide area. Huge trees such as these are extremely difficult to log, so young, smaller trees are sought for utilization, particularly those that are forest-grown and have long boles.

Although primarily a shade tree, monkey-pod also has potential as a timber tree. After the first year of planting at close spacings in Western Samoa, monkey-pod averaged 4 cm (1.6 in) d.b.h. and 4.4 m (14 ft) tall *(2)*. Because of its large crown, however, it requires wide spacing in plantations. A spacing of 2.4 by 2.4 m (8 by 8 ft) proved much too close in Zanzibar *(12)*. In Hawaii, two plantings at 3 by 3 m (10 by 10 ft) failed, possibly as a result of spacing, but more likely for lack of adequate tending. Monthly weeding around planted trees greatly improved height growth in the Philippines, thus ensuring survival *(6)*. Another planting in Hawaii that covered about 16 ha (40 acres) at 6 by 6 m (20 by 20 ft) was fairly successful and produced many trees with 7 to 10 m (24 to 32 ft), relatively straight, branch-free stems. The growth of this stand, now 85 years old, has never been measured or evaluated, however. Trees in this stand are 18 to 21 m (60 to 70 ft) tall and are about 91 to 122 cm (36 to 48 in) in diameter, and have crowns that are co-dominant in the overstory with *Eucalyptus*, *Ficus*, *Persea*, and other introduced trees that have invaded over the years.

Rate of growth depends on rainfall. In dry areas in Hawaii, diameter growth of open-grown trees is usually less than 13 mm (0.5 in) per year, and total height rarely exceeds 12 m (40 ft). In wet areas, diameter growth usually exceeds 2.5 cm (1 in) per year. An annual growth rate of 25 to 35 m^3/ha (350 to 500 ft^3/acre) was reported, but a source was not cited *(15)*. This rate may be excessive in view of the wide spacing required by this species.

Rooting Habit—Depth of rooting varies with amount of rainfall *(3,5)*. In dry areas with less than 1270 mm (50 in) annual rainfall, monkey-pod roots deeply. In wet areas, the root system develops at or near the soil surface and can become a problem in gardens or near paved roads.

Reaction to Competition—Monkey-pod is intolerant of shade. The leaves of shaded branches remain folded during the day and contribute little photosynthate. Shaded branches die back and improve the form of trees that shade each other.

Damaging Agents—Monkey-pod on the Island of Oahu, HI, is badly defoliated each year by three caterpillars, *Melipotis indomita*, *Ascalapha odorata*, and *Polydesma umbricola*, with most damage attributed to *M. indomita (13)*. The trees promptly leaf out after defoliation, so are not stressed for long. Stressed trees, however, are sometimes attacked by the monkeypod roundheaded borer *(Xystrocera globosa)*, which makes large galleries in the sapwood *(11)*. In Puerto Rico, ants *(Myrmelachista ramulorum)* bore into branchlets, resulting in defoliation and leaf deformation *(14)*. The defoliators can be controlled with insecticides applied to the tree trunks *(13)*. The tree is highly susceptible to leaf damage from herbicide overspray. Leaves are also very susceptible to damage by salt-laden mist from ocean storms (called 'ehu kai in Hawaiian).

Special Uses

The pods contain a sweet edible pulp that supplies nutritious food for animals. Children also chew on the pods, which have a licoricelike flavor *(3)*. Monkey-pod has long been a favorite of plant physiologists for studies of nyctinastic leaf movements *(9)*.

Although the tree is commonly used as a shade tree in parking lots, it is undesirable for this purpose because of the sticky flowers, gum, and seed pods that fall from it during much of the year.

Monkey-pod wood has been reported as hard and heavy *(12)*, and difficult to work *(3,4)*. Actually, in Hawaii and elsewhere in the Pacific where it has been used much more extensively than in its native habitat, the wood is considered easy to work, particularly because low shrinkage during drying allows it to be machined while green. Articles made from green wood can be dried without serious drying degrade *(10)*. In Hawaii, monkey-pod has been the premier craftwood used for carved and turned souvenir bowls since 1946. As labor costs increased, however, the industry spread to the Philippines and Thailand, which now supply most of the monkey-pod bowls for which Hawaii is famous.

Genetics

No information on the genetics of this tree was found. It is probable that the genetic base at each location where it has been introduced is quite narrow. For example, in Hawaii, the entire population may be the progeny of only two seeds, although the ease with which seed of this species can be transported in one's pocket from the Philippines, for example, makes this unlikely.

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Platanus occidentalis L. Sycamore

Platanaceae Sycamore family

O. O. Wells and R. C. Schmidtling

Sycamore *(Platanus occidentalis)* is a common tree and one of the largest in the eastern deciduous forests. Other names are American planetree, buttonwood, American sycamore, and buttonball-tree. It is a fast-growing and long-lived tree of lowlands and old fields. Sycamore is valuable for timber and is also widely planted as a shade tree because of its distinctive white, exfoliating bark and broad, dense crown. Recently, it has become a favored species for use in intensively cultured "biomass farms" in the Southeastern United States.

Habitat

Native Range

Sycamore (fig. 1) grows in all States east of the Great Plains except Minnesota. Its native range extends from southwestern Maine west to New York, extreme southern Ontario, central Michigan, and southern Wisconsin; south in Iowa and eastern Nebraska to eastern Kansas, Oklahoma, and south-central Texas; east to northwestern Florida and southeastern Georgia. It is also found in the mountains of northeastern Mexico.

Climate

Within the range of sycamore, average annual temperatures vary from 4° to 21° C (40° to 70 ° F), with average annual extremes from 41° to –34° C (105° to –30° F); the lowest temperature recorded was –40° C (–40° F). Average annual precipitation varies from 760 to 2030 mm (30 to 80 in), and the frost-free period is from 100 to 300 days. The natural occurrence of this species in eastern North America is probably limited in the North by frosts and low temperatures, and in the West by the dry climate of the Great Plains.

Soils and Topography

Sycamore is most common and reaches its largest size on alluvial soils along streams and in bottom lands. It is found most commonly on Entisols, Inceptisols, and Alfisols, and occasionally on Vertisols, Histosols, and Mollisols. The tree is tolerant of wet soil conditions, and in the northern part of its range it grows on the edge of streams and lakes and small depressions having slow drainage, as well as on wet muck land, shallow peat soils, and soils associated with river bottoms and flood plains. Farther south it commonly grows on the alluvial soils of flood plains adjacent to larger rivers, on former streambanks except in sloughs and swamps *(21)*, and in the moist coves, lower slopes, and ravines. In general, this tree grows best on sandy loams or loam with a good supply of ground water, typically on the edges of lakes and streams when the summer water table drops enough to permit good soil aeration during the growing season *(18)*. Sycamore is relatively intolerant of flooding during the growing season and will die if the entire tree is inundated for more than 2 weeks.

Sometimes sycamore is a pioneer tree on upland old-field sites. This is particularly true in the central part of its range. In the South, however, it rarely grows on old fields or even on well-drained ridges in the first bottoms.

Although sycamore becomes established on old eroded fields, it seldom grows well on these sites. On 60 old fields in southeastern Ohio, it was a minor constituent of the tree reproduction *(21)*. However, it is sometimes found in excellently stocked natural stands on coal-stripped land of the Central States. In Missouri, too, sycamore is often found in pure stands or in mixture with other hardwoods that volunteer on spoil banks *(21)*, and it is one of the pioneer species on the ridges of strip-mined land in Vermilion County, IL. It is recommended for planting on all types of coal-stripped land in many of the Northeast and Central States *(21)*.

In Tennessee, sycamore prospers in well-drained, gravelly and cherty, terrace soils, in a heavy weed cover *(21)*. It grows at elevations from just above sea level in some sections to 305 m (1,000 ft) in the northern part and 762 m (2,500 ft) in the southern part of the Appalachian Mountains. It also is found in coves, on lower east and north slopes, and on the moist soils of steep slopes and ravines facing major stream bottoms.

Associated Forest Cover

Sycamore grows singly or in small groups with other trees but seldom in extensive pure stands in the northern part of its range. In the Mississippi bottom lands of the South, however, it does grow in

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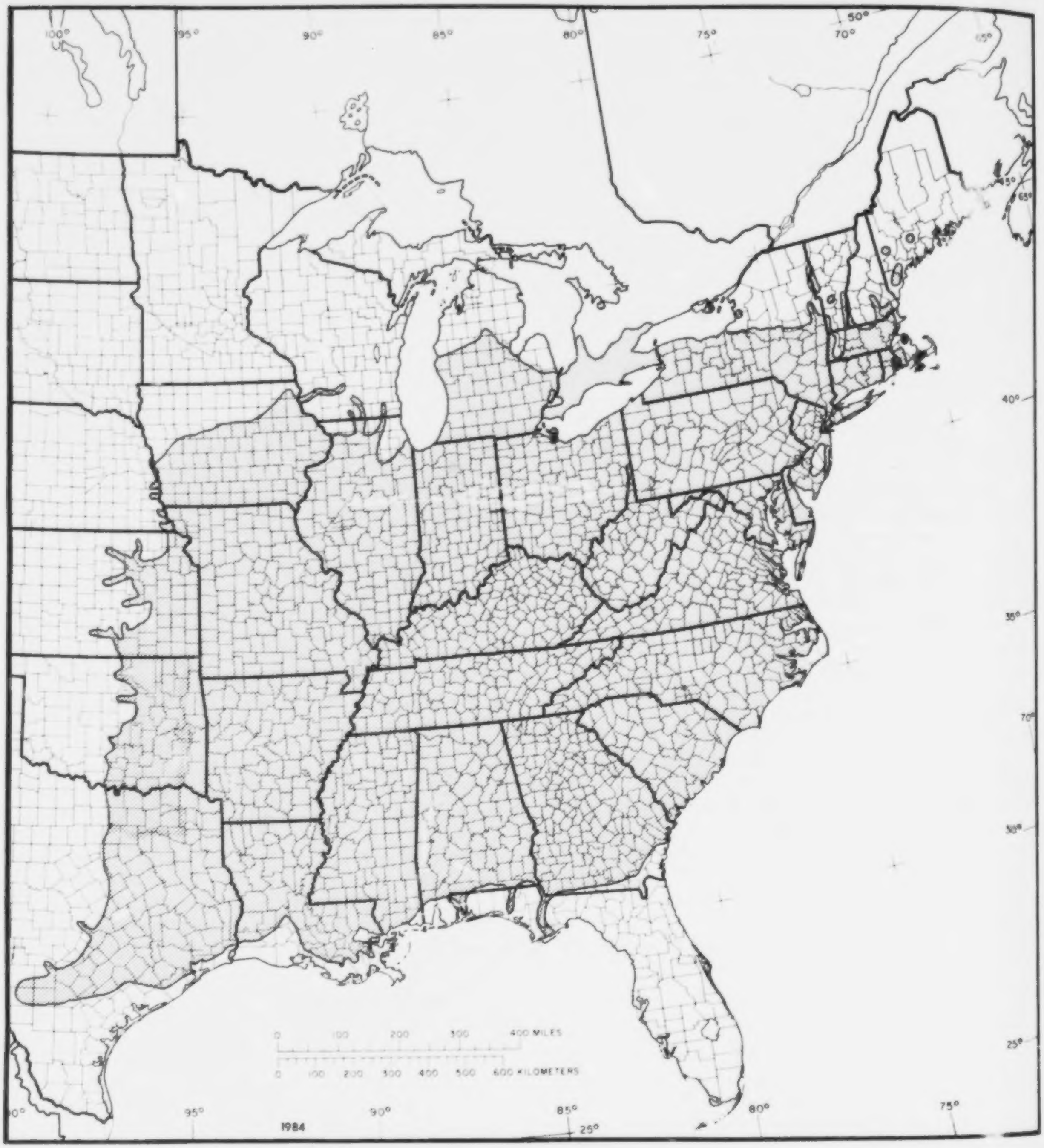
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Figure 1—*The native range of sycamore.*

pure stands of 16 to 40 ha (40 to 100 acres). Sycamore is the predominant tree in two forest cover types *(7)*. In River Birch–Sycamore (Society of American Foresters Type 61) the associate trees include sweetgum *(Liquidambar styraciflua)*, eastern cottonwood *(Populus deltoides)*, red maple *(Acer rubum)*, black willow *(Salix nigra)*, and other moist-site hardwoods. This type is widespread, occurring in southern New England, southern New York, New Jersey, Pennsylvania, southern parts of the Lake States and south into Oklahoma, Missouri, and Tennessee. It is also found in the Allegheny and Piedmont Plateaus of the Appalachian Mountains.

In Sycamore–Sweetgum–American Elm (Type 94), the chief associates are boxelder *(Acer negundo)*, green ash *(Fraxinus pennsylvanica)*, sugarberry *(Celtis laevigata)*, silver maple *(A. saccharinum)*, eastern cottonwood, black willow, water oak *(Quercus nigra)*, Nuttall oak *(Q. nuttallii)*, sweetgum, and river birch *(Betula nigra)*. This type is found throughout the southern part of the range of sycamore, usually on the alluvial flood plains of major rivers. A Sycamore–Pecan–American Elm variant type is found on river fronts in the Mississippi River Valley. A comprehensive survey of mixed hardwood species conducted in 14 Southeastern States by North Carolina State University showed that sycamore comprised 0.1 percent of the total basal area on wet flat sites, from 0.5 to 8.8 percent on various classes of bottom-land sites, 0.7 percent on lower slope coves, and 0.1 percent on upland slopes and ridges *(26)*.

Other forest types with which sycamore grows are Black Ash–American Elm–Red Maple (Type 39) in the northern part of the sycamore range, Sugarberry–American Elm–Green Ash (Type 93) in the South, Sweetgum–Yellow-Poplar (Type 87) in the Atlantic Coastal Plain and Piedmont, and Black Willow (Type 95), which grows throughout the range of sycamore.

Sycamore is also an important tree in Cottonwood (Type 63), a valuable pioneer type, characteristic of fronts on all major streams in the South except in sloughs and swamps *(21)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sycamore is monoecious. The male flower clusters grow on short stalks on branchlets of the previous year and the female flower clusters grow on short stalks on older branchlets. They appear in May in the North and as early as late March in the South. The fruit is a ball composed of many closely packed, long, narrow fruits that open by September or October and often remain on the tree over winter, breaking up or falling off the following spring. The seed is an achene with a light-brown, hairy, thin but hard seedcoat.

Seed Production and Dissemination—Plantation- or open-grown sycamore begins to bear seeds in 6 or 7 years. Dense natural stands begin to produce an appreciable number of seeds at about 25 years, with optimum production between 50 and 200 years. Generally, sycamore is not dependable for seed after the age of 250 years. The tree usually bears good seed crops every 1 or 2 years and some seeds are produced every year. Late spring frosts commonly kill the flowers, leaves, and even the twigs, reducing seed production *(21)*.

Sycamore seeds average about 441,000/kg (200,000/lb) and are dispersed from February through May of the spring following ripening. As the seed balls break up, the seeds are released and float down slowly. The hairs act as parachutes, and the seeds are widely scattered by the wind. Several birds feed on the seeds and also may disseminate them to a minor extent. Moreover, the seeds are carried by water and are often deposited on mudflats or sandbars where conditions are usually favorable for germination *(21)*.

Seedling Development—Pregermination treatments are not required *(3)*. A large percentage of sound seeds usually germinate, but the great variation in number of sound seeds in a lot results in a wide range of germinative capacity.

Germination is epigeal and is affected by light. In tests made at temperatures ranging between 23° to 27° C (73° to 81° F), the mean germination under artificial light was 17.5 percent and only 3.1 percent in the dark *(21)*. Seeds failed to germinate in the river-bottom soils of southern Illinois wherever litter was more than 2 inches deep. Sycamore seedlings must have direct light to survive; under favorable conditions they develop a strong, spreading root system and grow rapidly, as much as 91 to 122 cm (36 to 48 in) in height the first year. Roots also penetrate deeper in loess soil than in alluvial or clay soils.

Vegetative Reproduction—Sycamore sprouts readily from the stump when young (sapling or pole size) and the species has good potential for coppice regeneration, especially in short-rotation biomass plantings *(27)*. The best coppice reproduction has been obtained by late dormant-season March harvesting *(23)*.

Slips or cuttings made from young, fast-growing stems root readily and may be used for propagation. Healthier top growth has been noted on cuttings that were made closer to the root collars than other parts of the stem, and fall-planted cuttings grew better than those planted in the spring *(21)*. Cuttings from mature trees cannot be rooted by conventional methods, but a modified air-layering technique consisting of girdling and application of growth-promoting hormones on the tree before the cuttings are taken has been successful *(10)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Sycamore (fig. 2) grows fast throughout its life. Within its range, only cottonwood and, under some conditions, a few of the pines, soft maples, and black willow grow faster. Average 10-year diameter growth rates for sycamore of three size classes in five States were as follows *(21)*:

State	Seedlings and saplings	Pole-size trees	Sawtimber
	cm	*cm*	*cm*
Illinois	8.2	—	8.6
Indiana	8.9	6.6	6.4
Kentucky	6.0	6.9	8.1
Missouri	6.0	7.8	9.1
Ohio	7.4	3.6	6.0
	in	*in*	*in*
Illinois	3.2	—	3.4
Indiana	3.5	2.6	2.5
Kentucky	2.4	2.7	3.2
Missoun	2.4	3.1	3.5
Ohio	2.9	1.4	2.4

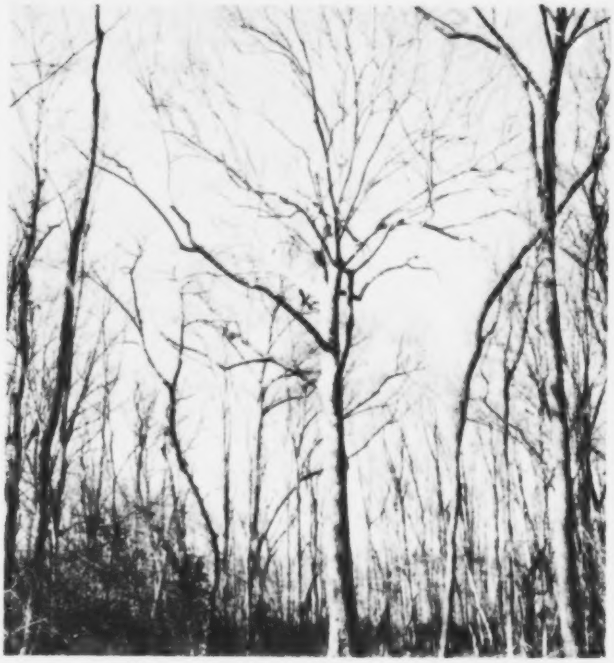

Figure 2—*A 40- to 50-year-old sycamore.*

These are average growth rates for a range of sites and should not be considered as indicative of growth that might be expected on either poor or good sites.

Sycamore in a 17-year-old North Carolina stand had an average d.b.h. of more than 23 cm (9 in) and an average height of 21.3 m (70 ft). There was a total volume of 126 m³/ha (1,800 ft³/acre) or 32.3 m³/ha (2,310 fbm/acre) of sawtimber plus 75.6 m³/ha (1,080 ft³/acre) of pulpwood. This stand was expected to have a volume of 140 m³/ha (10,000 fbm/acre) of sawtimber by age 22 *(21)*. This figure is slightly higher than average yield for mixed hardwoods in the southeastern United States. Annual hardwood yields in the major bottom-land type (where sycamore made up 8.8 percent of the stand) were found to average about 4.0 m³/ha (57 ft³/acre) in stands from 20 to 60 years old *(26)*.

The potential for plantation-grown sycamore seems much higher than the yields for natural stands. A survey conducted by North Carolina State University found that annual plantation yields ranged from 7.7 m³/ha (110 ft³/acre) at age 5, to 14.3 m³/ha (204 ft³/acre) at age 25 *(25)*. Most of the plantations in this survey were not cultivated to optimum intensity after establishment and in all likelihood do not represent the ultimate or even the practical maximum attainable yield.

Annual yield at age 11 in a sycamore plantation in central Georgia was 17.2 m³/ha (245 ft³/acre). Average d.b.h. was 15 cm (6 in) and average height was 19 m (63 ft) *(2)*. The highest yields for sycamore under intensive culture were recorded on a "creek bottom-land site" in the Georgia Piedmont *(14)* and in the lower Mississippi River Valley for 4-year coppice rotation following 3 or 4 years in seedling rotation *(6)*. Annual yields were from 24 to 32 m³/ha (343 ft³/acre). This yield is comparable to maximum yields obtained with other fast-growing genera such as *Populus* and *Alnus* that have been grown on "mini-rotations" *(4)*.

The American sycamore grows to a larger diameter than any other North American hardwood. Trees are on record that exceeded 305 cm (120 in) in d.b.h. and 43 m (140 ft) in height *(21)*. An individual tree in Indiana was 320 cm (126 in) in diameter at 1.2 m (4 ft) above the ground and 51 m (168 ft) tall *(21)*.

Open-grown sycamores have a large irregular crown that may spread to 30 m (100 ft) in diameter.

Under forest conditions the tree has a relatively small crown and a long, slightly tapered bole that may be clear of branches for 20 or 25 m (70 or 80 ft).

Rooting Habit—No information available.

Reaction to Competition—Sycamore is classed as intermediate in tolerance to shade and in competitive ability. It can compete successfully with cottonwood and willow, which it replaces or succeeds unless special steps are taken to favor these trees *(21)*.

In the Piedmont of North Carolina, sycamore and birch tend to replace pioneer trees like alder and willow on small islands or spits in streams after this land becomes stable and drained *(21)*. Sycamore and birch, in turn, are usually succeeded by elm *(Ulmus* spp.), ash, and red maple. It was found, however, that sycamore seedlings grown under controlled light were at least as tolerant as American and winged elm *(U. americana* and *U. alata)* on the basis of observed height growth and top-to-root ratios *(21)*.

On sand and gravel bars and on flood plains in Missouri, sycamore is a pioneer tree that persists throughout later successional stages in the sugar maple-bitternut hickory variant of Sugar Maple (Type 27) *(21)*. This variant grows on wet sites where the soils are usually neutral to calcareous.

Sycamore is also found in forest types that are pioneer, transitional, subclimax, and climax in the succession. On moist or wet sites in subclimax, deciduous forests it grows in association with oaks, black walnut *(Juglans nigra)*, hackberry *(Celtis occidentalis)*, sweetgum, cottonwood, and willow. It seems able to maintain itself in some of these subclimax and climax forest types because of its rapid growth and longevity. Usually it maintains a position in subclimax types only when they are in bottom land or other moist situations. On dryer sites sycamore usually has only pioneer or transitional status and is eventually replaced by tolerant trees or trees having less demanding moisture requirements.

Epicormic sprouting is not a serious problem in sycamore. Pruning widely spaced, open-grown natural trees 9 years old did not result in serious sprouting. In a Georgia thinning study, epicormic branching of sycamore was appreciable only where basal area was reduced to less than 18.4 m^2/ha (80 ft^2/acre), which was two-thirds or less of the original basal area. Heavier thinning resulted in 14 to 15 epicormic branches per tree *(21)*.

Damaging Agents—Many insects feed on sycamore but none are of economic importance in forests. Some may, however, seriously damage individual trees planted for landscaping purposes. Probably the insects that attack sycamore do not kill healthy trees, but when they attack a tree of reduced vigor, they may cause severe injury or death. The more important insects are the sycamore lacebug *(Corythuca ciliata)*, the flathead sycamore-heartwood borer *(Chalcophorella campestris)*, and the sycamore tussock moth *(Halisidota harrisii)*. Other insect enemies include leaf feeders and hoppers, periodical cicada *(Magicicada septendecim)*, aphids, scales, crosswood borers, flatheaded borers, roundheaded borers, bark borers, darkling beetles *(Tenebrionidae)*, ambrosia beetles, moths, and caterpillars, leaf rollers, and horntails *(Siricoidea)*. Sycamore is also subject to ant attacks, which often cause ingrown bark pockets that reduce the quality of the wood *(21)*.

Diseases of sycamore have become more important with its increased culture in plantations. In the mid-1970's, potentially serious infection involving leaf scorch, dead branches, top dieback, and lethal cankers occurred in Illinois and adjacent States *(22)*.

A 1973 survey of 26 plantations in Tennessee, Mississippi, Louisiana, and Alabama revealed leaf scorch, top dieback, and lethal bole cankers in four bottom-land plantations *(9)*. In two progeny tests in Mississippi the same symptoms were evident, so severely in one test that it was a total loss within 5 years *(5)*. The primary organism causing lethal bole cankers has not been established. A complex of organisms seems to be involved, but *Ceratocystis fimbriata* and *Botryodiplodia theobromae* are prime suspects. When seedlings were inoculated with either of these organisms by the bark-flap technique, cankers developed on the stem within 30 days; when 8-year-old trees were inoculated with *Ceratocystis fimbriata*, cankers appeared and some trees died within a year *(19)*. Temperature also seems to be a factor *(15,16,17)*. *Acremonium diospyri* has also been identified in trees displaying these symptoms.

Sycamore is susceptible to anthracnose, the same disease that attacks oaks *(21)*. This fungus attacks in the spring and sometimes completely defoliates the trees. Severe attacks also kill twigs, and frequently cankers are formed up to 25 mm (1 in) in diameter. Usually, a second set of leaves is produced following defoliation and few trees die from an attack. Anthracnose may weaken a tree, however, making it susceptible to attack by other diseases. Heavy attacks by this disease also reduce radial and terminal growth. Sycamore is host to the eastern mistletoe *(Phoradendron* spp.) but damage usually is not serious.

Weather damage and damage caused by insects and disease are commonly confused. For example, anthracnose attacks are often mistaken for frost damage. Although low winter temperature may injure the cork cambium and cause the outer bark to be sloughed off, the health of the tree is not affected. Late spring frosts may kill sycamore buds over a wide area, and where this occurs, the damaged trees characteristically have long dead twigs with bushy masses of leaves around their bases by midsummer.

A limited study of sycamore shade trees following a sleet storm in west-central Illinois indicated that the tree is susceptible to ice damage *(21)*. But in forest stands, it is seldom damaged by such storms.

Because it develops a widespread, strongly branched root system, sycamore is a windfirm tree. However, large sycamores are likely to develop windshake, a wood defect that reduces their value for lumber and other products.

Special Uses

Establishment of sycamore plantations increased during the 1960's and 1970's. As of 1979, about 1500ha/yr (3,700 acre/year) were being planted to sycamore of a total 4170 ha/yr (10,300 acre/yr) of hardwoods planted in the Southeast *(30)*. In general, establishment of these plantations has been characterized by intensive site preparation, cultivation and fertilization for several years after planting, high initial costs, and fast growth. Sycamore has fast initial growth rate on a wide range of sites, including relatively infertile "pine" sites. After only a few years, however, its growth declines and it stagnates on the less fertile sites unless fertilizer is added.

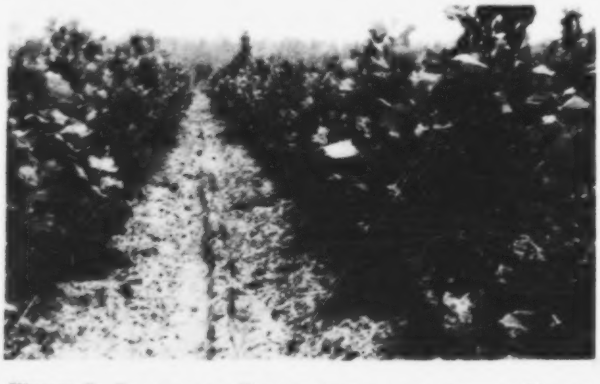

Figure 3—*Sycamore seedlings in first growing season in Georgia Coastal Plain, short-rotation planting. Spacing is 1.2 by 2.4 m (4 by 8 ft).*

Some plantations have been established at very close spacing and are being reproduced by coppice on short rotations in a silvicultural scheme aimed at maximum fiber production (fig. 3). This kind of culture has been termed "short-rotation forestry" *(27)* or "silvicultural biomass farms" *(11)*. The entire aboveground portion of the plant is harvested and estimates of annual biomass production in parts of the United States range from 11.2 to 29.1 dry ton equivalents/ha (5 to 13 dry ton equivalents/acre) at rotations of 4 to 10 years *(4)*.

Nutrient drain on the site is greater than with conventional long rotation management *(1,[illegible])* and fertilization is usually necessary, especially with rotations shorter than 5 years *(28)*.

In spite of the high initial cost, one analysis in the Coastal Plain of Virginia and North Carolina estimated that over a 36-year period (three 12-year coppice rotations) total yield of four hardwood species including sycamore would be increased at least 50 percent over natural stands at one-third the cost of a system of natural regeneration *(20)*.

Genetics

Genetic experiments with sycamore in the eastern United States have demonstrated heritable variation in growth and other traits *(8,13,24,29,31)*. Tree improvement programs are in progress *(20)* and genetic gains in early growth rate have been obtained *(13,31)*.

Geographic variation in sycamore is extensive, and, noted in many other widely distributed species, trees of southern origin have a potential for faster growth than trees of more northern origin when planted near or slightly north of their point of origin *(8,13,24,29,31)*.

Sycamore is unique among North American tree species in displaying a strong north-south gradient in resistance to a killing stem canker disease. In two progeny tests of half-sib families selected along the Mississippi and Chattahoochie Rivers, families of northern origin (Missouri and northern Georgia) were attacked much more severely than were families from farther south (southern Georgia and Louisiana) *(5)*.

Two varieties of sycamore have been named in addition to the typical variety. *P. occidentalis* var. *glabrata* is common in western Texas and Mexico but is considered by some taxonomists to be synonymous with the typical variety. *P. occidentalis* var. *attenuata* is apparently intermixed with the typical variety, but its status is in need of clarification. The London plane of the Old World, *P.* × *acerifolia*, is considered a collection of advanced generation hybrids and backcrosses between *P. orientalis* and *P. occidentalis* *(12)*. London plane is an important street tree in cities of the United States and Europe because of its resistance to diseases and especially the air pollution found in the urban environment.

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Populus balsamifera L. Balsam Poplar

Salicaceae Willow family

John C. Zasada and Howard M. Phipps

Balsam poplar *(Populus balsamifera)* is the northernmost American hardwood. It grows transcontinentally on upland and flood plain sites but attains the best development on flood plains. It is a hardy, fast-growing tree which is generally short lived, with some trees reaching 200 years. Other names are balm-of-gilead, bam, tacamahac, cottonwood, or heartleaf balsam poplar. Many kinds of animals use the twigs for food. The light, soft wood is used for pulp and construction.

Habitat

Native Range

The range of balsam poplar (fig. 1) spans about 110° in longitude (55° to 165° W.) and 26° in latitude (42° to 68° N.). It extends across North America along the northern limit of trees from Newfoundland, Labrador, and Quebec west to Hudson Bay and northwest to Mackenzie Bay. From northwest Alaska, its range extends south to southwest Alaska and part of southcentral Alaska, north and east British Columbia; east to southeast Saskatchewan, east North Dakota, northeast South Dakota, Minnesota, Wisconsin, northwest Indiana, Michigan, southern Ontario, New York, and Maine. It is local in the western mountains, south to northeast Oregon, Idaho, extreme northern Utah, central Colorado, extreme northwest Nebraska, and the Black Hills of South Dakota and Wyoming. It is also scattered in northern Iowa, northeast Ohio, Pennsylvania, northern West Virginia, extreme eastern Maryland, and northwestern Connecticut.

Climate

Most of the range of balsam poplar has a continental climate, but some is in the maritime zone and the transition between these two broad regions. Average temperature ranges from -30° to -4° C (- 22° to 25° F) in January and from 12° to 24° C (53° to 75° F) in July. The lowest temperatures range from -18° to -62° C (-10° to -79° F); the highest from 30° to 44° C (85° to 110° F). Annual precipitation is lowest in central Alaska (15 to 30 cm; 6 to 12 in) in the Yukon–Tanana drainage. The highest precipitation, 140 cm (55 in), occurs in the Maritime Provinces of eastern Canada. Distribution of precipitation varies throughout the range, but prolonged summer droughts are uncommon. Annual snowfall is lowest in interior Alaska (100 to 200 cm; 40 to 80 in) and highest in Newfoundland (400 cm; 160 in). Maximum summer daylength varies from 16 to 24 hours. Minimum daylength in winter drops to zero above the Arctic Circle. The frost-free period varies from 75 to 160 days. The longest growing seasons are in the southern part of the range and the shortest in the north, but growing seasons can be 120 days in parts of Alaska.

Soils and Topography

Maximum development of balsam poplar stands occurs on the river flood plains in Alaska, Yukon Territory and Northwest Territories, British Columbia, and Alberta. Balsam poplar can become established shortly after formation of a sand or gravel bar. At 15 to 25 years after site formation, it assumes dominance and retains it for 50 to 75 years, disappearing 100 to 200 years after site formation *(40,51)*. During stand development, depth of medium to fine sand and silt-textured material accumulates from a few centimeters to as much as 2 to 3 m (6.6 to 9.8 ft). Periodic flooding occurs at spring breakup and in later summer—sometimes both; duration and degree of flooding depend on terrace height and distance from the river *(40)*. The soil that develops consists of river sediment and organic matter in alternating layers of variable thickness. In northeast British Columbia, average annual rate of sediment accumulation was estimated to be 6 to 10 cm (2.4 to 3.9 in) from site age 0 to 50; beyond age 50, accumulation was estimated at 8 mm (0.3 in) *(40)*. Balsam poplar grows primarily on soils of the order Inceptisols and, to a lesser extent, of the order Entisols.

Before balsam poplar becomes dominant on a site, the river is the predominant influence on soil development. As balsam poplar becomes dominant, the vegetation becomes of equal importance in soil development *(50,51)*. This results from the continuous aerial plant cover and increased litter (leaf) fall and decreased rate of siltation. In the balsam poplar stage, (a) forest floor nitrogen content increases while soil nitrogen remains relatively constant; (b) soil carbon and cation exchange capacity

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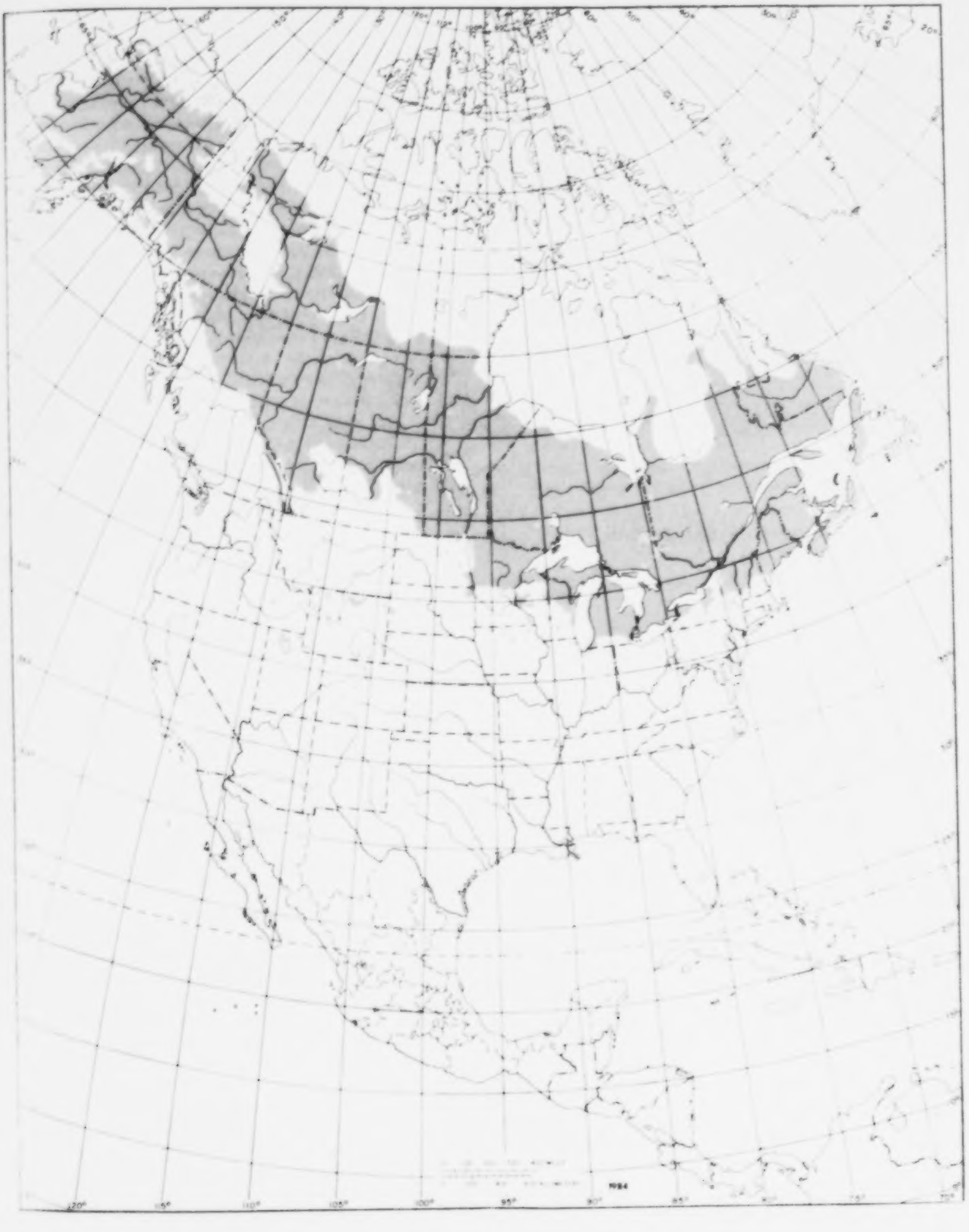
120°
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Figure 1—*The native range of balsam poplar.*

Figure 2—*Mature balsam poplar stand growing at the confluence of the Chulitna and Susitna Rivers in south-central Alaska.*

increase; (c) sulfate concentration, the major component of a salt crust common in early stages of succession, declines; and (d) depth and importance of the forest floor increases *(51)*.

Soil temperatures in balsam poplar stands are cooler than in earlier stages of succession but warmer than the white spruce stands that succeed them. Soils are usually thawed to a depth of 1.5 m (4.9 ft) or more by May. Soil temperatures during the growing season vary from 8° to 14° C (46° to 57° F) *(53)*. Permafrost has been reported on only the most northern sites; for example, permafrost is found at a depth of about 1 m (3.3 ft) during the growing season along the delta of the Mackenzie River, where summer soil temperatures in the surface 0.5 m (1.6 ft) range from 2° to 10° C (36° to 50° F) during the growing season *(18)*. On Alaska flood plain sites, soil pH was 6.9 to 8.2; nitrogen, 0.6 to 0.01 percent; phosphorus, 7.0 to 0.3 parts per million; and cation exchange capacity, 13.1 to 5.6 me/100 g *(66)*.

The roots of balsam poplar in young stands can extract water from near the water table and the capillary zone above it. As stands age, the importance of water supplied by rain and snow increases.

In the eastern portion of the range and on upland sites in the west portion, balsam poplar occurs on soils developed from lacustrian deposits, glacial till, outwash, and loess. In Saskatchewan, it is frequently associated with aspen on moderately well-drained sites, but its distribution is usually restricted to local depressions or drainage channels *(10,31)*. A higher proportion of balsam poplar relative to aspen in the white spruce-feathermoss ecosystem indicates sites that have excess water in early spring *(31)*. It was the only one of seven boreal tree species that was associated with clay soils and was found on poorly drained sites having a pH greater than 7.2 *(10)*. Balsam poplar grows in "hotter" ecoclimates and "fresh" to "wetter" soils in the moderate, humid site regions of eastern and central Ontario. In moist, subhumid western Ontario, it most commonly occurs on fresh to wetter soils in the areas of "normal" ecoclimate. In Ontario, balsam poplar occurs on sites that are relatively rich in nutrients and less acidic *(19)*. In the open, subarctic woodlands in northern Ontario, balsam poplar and white spruce form the only closed forests, and these grow in river bottoms *(5)*. Balsam poplar grows on dry, sandy, southfacing sites near treeline in Canada.

The northernmost balsam poplar stands are associated with warm springs that arise in the northern foothills of the Brooks Range in Alaska. This area is in the zone of continuous permafrost, and these stands are forested islands in a sea of arctic tundra.

Associated Forest Cover

Balsam poplar occurs in the following forest cover types *(13)*: Balsam Poplar (Society of American Foresters Type 203), White Spruce–Aspen (Type 251), White Spruce (Types 107 and 201), Jack Pine (Type 1), Aspen (Type 16), Red Spruce–Balsam Fir (Type 33), Northern White-Cedar (Type 37), Black Ash–American Elm–Red Maple (Type 39).

In eastern North America, balsam poplar is found mainly in mixed stands where other species dominate. In Saskatchewan, it is a component of the following forest types: Aspen-hazelnut *(Populus tremuloides/Corylus cornuta)*, white spruce *(Picea glauca)*-feathermoss, aspen-sarsaparilla *(Aralia nudicaulis)*/twinflower *(Linnaea borealis)*, white spruce/aspen-bunchberry (Cornus canadensis)/bishops cap *(Mitella nuda)*, black spruce *(Picea mariana)*-feathermoss, and white spruce-horsetail (*Equisetum* spp.) *(31)*. Balsam poplar is uncommon in boreal white spruce forests east of about 75° longitude and is not present in black spruce stands east of 85 to 86° longitude. It grows with white spruce east of 75° longitude, however *(45)*. Other associated trees are balsam fir *(Abies balsamea)*, paper birch *(Betula papyrifera)*, black ash *(Fraxinus nigra)*, American elm *(Ulmus americana)*, red maple *(Acer rubrum)*, tamarack *(Larix laricina)*, and northern white-cedar *(Thuja canadensis)*.

In western and northern parts of the range, balsam poplar is associated with balsam/alpine fir *(Abies lasiocarpa)*, aspen, paper birch, white spruce, and black spruce on upland sites. It reaches its most widespread development on the river flood plains. On these sites, it occurs in pure stands and is associated with mountain alder (*Alnus incana*) and various willows (e.g., *Salix alaxensis, S. interior*) during early stand development and white spruce in later stages when it finally disappears from these sites (*53,57*).

Low shrubs associated with balsam poplar include red-osier dogwood (*Cornus stolonifera*), bunchberry, mountain maple (*Acer spicatum*), bearberry honeysuckle (*Lonicera involucrata*), beaked hazel, American cranberry bush (*Viburnum trilobum*), highbush cranberry (*V. edule*), red raspberry (*Rubus idaeus* var. *canadensis* and *strigosus*), prickly rose (*Rosa acicularis*), mountain cranberry (*Vaccinium vitis-idaea*), devil's club (*Oplopanax horridum*), and red currant (*Ribes triste*).

Some associated herbaceous plants are horsetails (*Equisetum arvense, E. pratense*), bluejoint reedgrass (*Calamagrostis canadensis*), bedstraws (*Galium boreale, G. triflorum*), fireweed (*Epilobium angustifolium*), panicle bluebells (*Mertensia paniculata*), red baneberry (*Actaea rubra*), alpine pyrola (*Pyrola asarifolia*), claspleaf twistedstalk (*Streptopus amplexifolius*), wild sarsaparilla, butterbur (*Petasites* spp.), and bishops cap.

In mixed stands, various feathermosses (e.g., *Hylocomium splendens, Pleurozium schreberi*) and lichens may be associated with balsam poplar. In Alaska, two mosses, *Eurhynchium pulchellum* and *Mnium cuspidatum*, have been reported in flood plain stands (*53*). Moss and lichen cover is generally low in these stands.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Balsam poplar generally reaches flowering age between 8 and 10 years. It produces large seed crops almost every year, but significant annual variation in production can occur by individual stands and trees (*47,59*). Flowering in this dioecious species occurs before leaf flush, in April and May throughout most of the range, but not until June or July at northern limits and upper elevations.

The regional ratio of male to female clones was found to be 1:1 on treeline sites in northern Quebec. Female clones occurred on sites with a relatively milder climate or those that were more fertile and mesic; male clones were more common on inland sites with drier soil conditions. Most stands were made up of more than one clone; however, monoclonal stands usually contained a male clone, and polyclonal stands usually had only female clones. Stand density and area were greater in male than in female clones (*6*).

Flower clusters (catkins) are 5 to 9 cm (2 to 3.5 in) with many small flowers about 3 mm (0.12 in) long. Male flowers have 20 to 30 reddish stamens. Mature female catkins are 10 to 15 cm (4 to 6 in) long. Capsules are a lustrous green during development but turn dull green at time of dispersal. Male flowers are shed promptly and decay; female catkins are shed shortly after dispersal is completed but remain identifiable for the remainder of the summer (*2,56*).

Seed Production and Dissemination—Seeds are tan and small (0.3 mg or 0.005 gr); they do not have an endosperm at maturity. Dispersal begins in May and June throughout most of the range, but dissemination can occur through the last week of July in northernmost stands (*33,59*). Dispersal of seeds lasts for at least 2 weeks. Viable seeds are found on trees 4 to 6 weeks after the start of dispersal in some years. Relatively warm, dry weather causes rapid dispersal. Each small seed is attached to a tuft of long, silky hair ideally suited for long distance dispersal by the wind. Under warm, dry conditions, seeds are frequently carried upward by convection currents. Large quantities of seeds fall within the stand, however, and large numbers of short-lived germinants can be found on suitable substrates in mature stands (*59*). On flood plain sites, large quantities of seeds land in water and may be carried long distances by rivers. Seeds sink rapidly, however, when detached from the silky hairs.

Although most balsam poplar seeds die within several weeks of dispersal, some remain viable for 4 to 5 weeks. Duration of viability is dependent on temperature and moisture; cooler, drier conditions prolong viability. Viability can be maintained at 90 percent or greater for at least 3 years when seed is stored in airtight containers at -10° C (14° F) (*4,63,65*).

Seedling Development—The seed does not exhibit dormancy, and germination occurs over a wide range of temperatures (5° to 35° C; 41° to 95° F) provided moisture is adequate (*63*). Germination can occur under water, and even mild water deficits reduce germination (*33*). Germination is reduced by exposure to the concentrations of salt that commonly occur as crusts on river flood plains (*33*). In a comparison of germination on different types of naturally occurring substrates, balsam poplar germinated over a wider range of substrate moisture content on sand-algal crusts than on silt, sand, or silt-salt crust substrates (*33*). Complete germination occurs in the dark and over a range of overstory conditions *(59)*. Burial of seed up to several millimeters does not prevent germination but reduces it.

Germination is epigeal and can occur after the seed has separated from the silky hair or in association with the hairs. Under ideal conditions, germination is rapid, and cotyledons can be expanded in 18 to 24 hours *(33,64)*. The rate of germination declines below 15° to 20° C (59° to 68° F) *(64)*. A conspicuous ring of fine hairs is formed at the root-hypocotyl junction. These hairs anchor the seedling to the substrate until the radicle provides a more substantial foothold. Moist mineral soil surfaces are the best seedbeds. Seeds germinate on moist organic seedbeds, but seedling survival is poor, and most seedlings die soon after germination *(6,59,67)*.

Seedling development depends on photosynthesis soon after germination. After the first growing season, hypocotyl length varies from 2 to 5 mm (0.08 to 0.20 in) under Alaska conditions. Tricotyledonous seedlings do occur, but they are rare. Albinism can be as high as 5 percent in some seed lots in Alaska. Leaf production begins with the development of two leaves separated by 0 to 4 mm (0 to 0.16 in); the first leaf is 1 to 3 mm (0.04 to 0.12 in) above the cotyledons. Subsequent leaf production and internode development vary by microsite and with seedling density, with maximum production of 11 leaves under field conditions in Alaska. The third and fourth internodes are the longest *(25)*.

The height and dry weight of first-year seedlings are affected by density *(25,39)*. Seedlings grown in a greenhouse from an Ontario seed source ranged from 5 to 32 cm (2 to 12.5 in) in height and 11 to 220 mg (0.17 to 3.4 gr) per plant as density decreased from about 59,000 to 323 seedlings/m^2 *(39)*. Seedlings grown under normal environmental conditions in interior Alaska ranged from 2 to 6 cm (0.8 to 2.4 in) tall at sowing densities ranging from 73,400 to 1 seeds/m^2 (6,820 to 0.1/ft^2). First-year shoot growth was proleptic with no branch formation unless the apex was damaged. Dry weight of leaves and stems ranged from 20 to 520 mg (0.3 to 8.0 gr) *(25)*. Average root length varied from 9 to 13 cm (3.5 to 5.1 in).

On flood plain sites, height growth of planted seedlings in early successional stages was twice that in later stages. Growth appeared to be controlled by nitrogen availability in some stages of succession and a combination of light, water, and nutrient availability in other stages. In greenhouse studies, balsam poplar seedling biomass was greater on soils from alder stands than on those from earlier successional stages, suggesting that poplar benefits from nitrogen fixation. The growth of seedlings on early successional soils increased significantly when they were fertilized, but growth on alder soils was not affected by fertilization *(58)*. Natural seedlings were found only in the early successional stages, and growth rate was similar in each of these stages.

Vegetative Reproduction—Balsam poplar is one of the most versatile members of the Salicaceae in its potential for vegetative reproduction. New stems originating from intact or broken roots, preformed or adventitious buds on stumps or at the base of trees, and buried stems or branches have been observed in primary or secondary succession on flood plain and upland sites *(33,66,69)*.

In Alaska, segments of stems and branches broken and buried during autumn logging contribute to regeneration. This buried material was from 2 to 6 cm (0.8 to 2.4 in) in diameter and 10 to 200 cm (4 to 79 in) long *(69)*.

Dormant hardwood stem cuttings, as old as 10 to 15 years and probably older, will produce roots and new shoots. Older cuttings frequently take longer to root than younger cuttings. The distal portion of the current year's growth may root more poorly than the basal part of the current growth and 2-year-old wood. In a rooting study conducted with material from Ontario, cuttings collected after December had a higher percentage of rooting, more roots per cutting, and a higher percentage of cuttings with bud activity than those collected before December. Age of the parent tree had no effect on number of roots produced or bud activity (8). Clonal differences are a major source of variation in rooting percentage and the number of primary roots produced by dormant cuttings *(15)*. Rooting potential for hardwood cuttings ranges from 75 to 100 percent *(8,24)*; rooting of softwood cuttings ranges from 23 to 63 percent, depending on treatment *(24)*.

Unrooted stem sections have been used with varying success in regeneration of field sites. In one study in Alaska, survival after 3 years ranged from 15 to 82 percent. Highest survival was observed on gravel substrates, least on silt and sand soils. Third-year height was greatest on silt and sand—1.2 m (3.9 ft) *(28)*. In a prescribed burn, survival after 5 years was generally low; microsites burned to mineral soil supported the best growth. Relatively deep organic layers, whether burned or unburned, provide a poor environment for the establishment of unrooted stem cuttings *(65,66)*.

Stem cuttings (hardwood and softwood or greenwood cuttings) have been the major means of stand establishment for the short-rotation intensive culture of balsam poplar and hybrid poplars in Wisconsin, Ontario, and other areas *(20)*. Hardwood cuttings are grown in clonal orchards, harvested, stored and planted either rooted or unrooted. Clones that are difficult to root may survive better if they are regenerated from rooted cuttings. Greenwood cuttings provide a means of rapidly increasing the number of desirable clones, but they must be rooted before planting *(20)*.

In the greenhouse, root cuttings of balsam poplar clones from Utah produced surface suckers from suppressed buds and end suckers from the cambium at the cut end *(46)*. Root cuttings also produce new lateral roots from the same origins as suckers. Alaskan clones respond similarly *(69)*.

Production of suckers after disturbance of the parent tree varies; the response is generally less than that of aspen which suckers prolifically. In Alaska, stocking after 3 years ranged from 4 to 61 percent; densities were 1 to 2 plants/m^2 (3 to 8/milacre) in harvested balsam poplar stands. Suckers made up about 80 percent of the stocking in the summer- and winter-logged areas but only 27 percent in a fall-harvested area. Production was on intact and broken roots within the upper 2 cm (0.8 in) of the surface soil. Average diameter of roots producing suckers was 1 cm (0.4 in) *(69)*. In a 40- to 50-year-old stand on the Tanana River in interior Alaska, stocking was 83 percent and density 2 trees/m^2 (8/milacre) *(25)*. In Saskatchewan, sucker regeneration was observed on dry, moist, and wet regimes. Stocking was 12 percent in the aspen-hazelnut type; 5 percent in the white spruce aspen-bunchberry type; 5 percent in the white spruce/feathermoss type; and 7 percent in the aspen/sarsaparilla/twinflower type *(31)*.

Density of suckers is greatest on sites where the organic layers are disturbed. Organic layers are effective insulators and may limit sprouting by controlling soil temperature, particularly in high latitude forests *(69)*.

Production of suckers may be important in the invasion and establishment of balsam poplar on disturbed sites and in primary succession. Expansion has been observed on flood plains from established stands to areas that did not have poplar *(40)*. Colonization by clonal expansion is believed to be more important on dry sites where the probability of seedling establishment is low *(33)*. The area covered by individual clones on productive forest sites is not well documented; one 15-year-old clone consisted of 27 ramets and covered an area of 350 m^2 (3,700 ft^2) *(33)*.

The extent of clonal development is best documented at elevational and latitudinal treeline sites where seedling establishment is limited and development of stands through vegetative growth is the main means of colonization and maintenance of the species *(6,35)*. Scattered groves of balsam poplar in the Brooks and Alaska Ranges of Alaska were found to be individual clones. Representative clones covered from 100 to 200 m^2 (1,060 to 2,110 ft^2) and contained from 90 to 150 ramets. Clones with the oldest ramets (114 years old) were found on the Brooks Range sites. Ramets did not occur in areas with dense shrub cover *(35)*.

New shoots also form on stumps from suppressed buds and adventitious buds developed from undifferentiated inner bark. Most originate in the inner bark at the top of the stump. Sprouting response varies with genotype and declines as tree age increases. It may be high (50 to 100/stump) initially, but production and survival of sprouts vary with season and logging method. The percentage of stumps with sprouts declines over a 2- to 5-year period *(69)*.

Balsam poplar stump sprouts may be of little potential value in replacement of trees in mature stands after disturbance because of the fragile connection between sprout and stump. In intensively cultured stands grown on short rotations, coppicing is used to replace the new crop after harvest of the original stand established from stem cuttings. Individual cuttings may produce 10 to 20 sprouts 1 year after harvesting; 4 to 8 sprouts will survive after 2 years *(20)*.

The growth potential of balsam poplar vegetative reproduction is greater than that of early seedling growth. Average height of balsam poplar was about 1 m (3.2 ft) after 3 years; height of dominants was 2.5 to 3.0 m (8.1 to 9.8 ft). The age of suckers at breast height (1.5 m or 4.9 ft) varies with site quality and the degree and type of disturbance *(21,25)*.

The most detailed data available for growth of vegetative reproduction comes from stands of a *P. balsamifera* × *tristis* hybrid established from stem cuttings. After harvest of the original stands, coppice stands are managed for several rotations. Mean annual increment (stem plus branchwood) is 21 to 25 t/ha (9.5 to 11.0 tons/acre), depending on stand age and rotation length *(11)*. Other studies with this hybrid have shown that 1- and 2-year-old coppice stands are taller and more productive than stands of similar age established from stem cuttings. Architecturally, the stands are different in that each individual in coppice stands has 10 to 20 stems at age 1 and 4 to 8 stems at age 2. Stands from stem cuttings usually contain one stem per individual at this age *(20)*.

Internode length on young vegetative regeneration is usually greatest in the lower part of the annual shoot. Buds are longest in the central part of the shoot, and the terminal bud is equal to the largest nodal bud. First-order branches are smallest at the base of the previous year's growth and longest near the top. Angle of divergence of first-order branches is 30° to 40° *(37)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Large balsam poplar throughout much of the range may be 90 to 180 cm (35 to 71 in) in diameter and 23 to 30 m (75 to 100 ft) in height *(44)*. In the northern part of the range, this species is frequently the largest tree in 80- to 100-year-old stands. Beyond this age, conifers, which eventually replace balsam poplar, usually attain greater heights but not necessarily larger diameters (fig. 3).

The form or branching pattern of young trees is excurrent, with a clearly defined main bole and conical crown. In the 80- to 100-year-old age class, trees tend to have a more rounded crown, however, and the central stem gives rise to a more deliquescent or decurrent growth habit. On good sites the excurrent growth habit is present to at least 40 to 50 years. On poorer sites, the decurrent growth habit may occur earlier. The branching system is composed of long and short shoots; short shoots produce most of the leaves. Long shoots account for height growth and lateral branch extension.

Balsam poplar vegetative buds exhibit unconditional dormancy in the fall and early winter. A brief chilling period removes this dormancy, however, and by early February, buds are largely in a state of imposed dormancy with active growth commencing as soon as the temperature is high enough *(14)*.

Specific gravity of balsam poplar wood ranges from 0.326 to 0.346 and differs among sites. Within individual trees, specific gravity varies from 0.318 to 0.429 and is greatest at the top of the tree. Fiber length ranges from 1.02 mm (0.04 in) at breast height to 0.78 mm (0.03 in) at a bole position of 75 percent of total height. Sapwood pH averages 5.40 and heartwood 8.12. No significant differences were found among male and female clones in pH or wood and bark extractives. Lignin content of wood was higher in the sapwood than in the heartwood; bark lignin content was three times greater than that of the wood *(32,48)*.

Balsam poplar stands are generally even-aged, with some variation. On upland sites in Saskatchewan, the greatest age span is about 17 years, but most stands have an age range of 5 years or less *(10)*. Age spans are 20 to 25 years or less in young stands and 50 to 60 years in 155- to 165-year-old stands occupying flood plain sites in northeast British Columbia *(40)*.

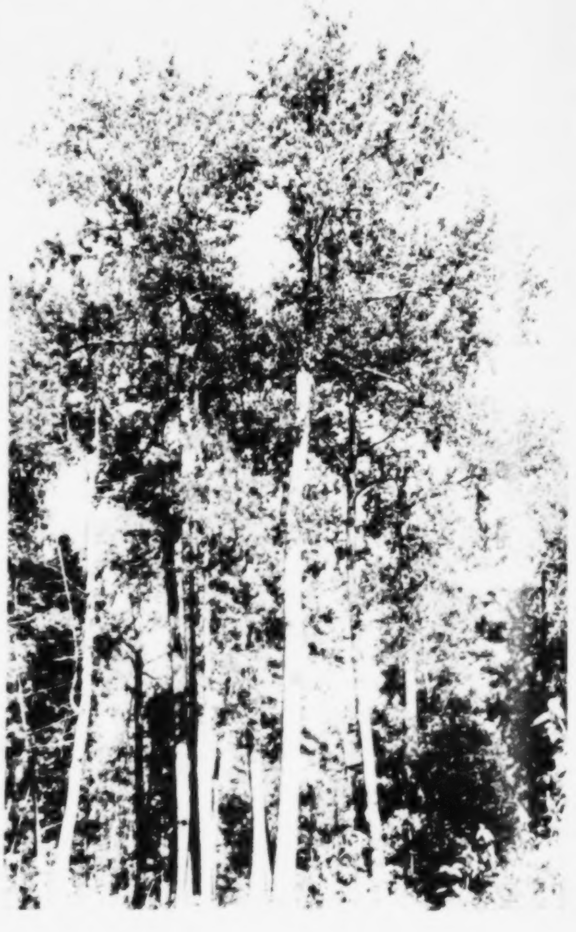

Figure 3—*Mature balsam poplars 41 cm to 51 cm (16 to 20 in) in d.b.h. in Minnesota—about 100 years old.*

The greatest age spans have been observed in the poplar groves characteristic of treeline stands. Clones in Alaska treeline stands have ramets ranging in age from 1 to more than 100 years old. New suckers tend to be produced at the periphery of the clone *(35)*.

Stand density varies with stand history. The density of stems larger than 2.5 cm (1 in) varies from 8700/ha (3,250/acre) in 25-year-old stands to 225/ha (91/acre) in 200-year-old stands *(53)*. In southern portions of the species' range, stand density is not well documented but is probably lower than in northern areas because balsam poplar does not normally occur in large pure stands. In Wisconsin, balsam poplar

Table 1—Density and volume of balsam poplar in Saskatchewan by site type and drainage (adapted from *23*)

Site type and drainage	Density			Volume		
	trees/ha	*trees/acre*	*Pct of stand*	*m²/ha*	*ft²/acre*	*Pct of stand*
White spruce-feathermoss, well drained	17	7	3	11	157	5
White spruce/aspen-bunchberry, well drained	86	35	7	14	200	7
Aspen-hazelnut, well drained	91	37	12	22	314	10
Jack pine-feathermoss/[illegible] moss, moderately well drained	7	3	1	2	26	1
White spruce-feathermoss, moderately well drained	44	18	6	25	357	8

made up less than 2 percent of the total stand volume in the types where it was present (for example, balsam fir-white spruce, aspen, and tamarack) *(12)*. In mixed-wood sections, balsam poplar makes up 7 percent of the total volume and annual growth *(31)*, but this percentage varies with site type and drainage (table 1).

Total balsam poplar biomass estimates in Alaska range from 75 t/ha (33 tons/acre) in the Yukon River drainage to 180 t/ha (80 tons/acre) on the Tanana River flood plain for 60-year-old stands *(29,68)*. In Alberta, aboveground dry weight for trees 16 to 65 years old varied from 0.45 to 251 kg (0.99 to 553 lb); 33 to 71 percent of this weight was in the main stem *(30)*.

Forest survey reports for Alaska indicate that, in unmanaged stands, balsam poplar (or the hybrid with *P. trichocarpa*) has a mean annual increment of from 4 to 6 m³/ha (57 to 86 ft³/acre) in the Susitna Valley. Site indices (base age 100 years) in British Columbia range from 6 to 12 ft (low) to 34 to 42 ft (good) *(21)*.

Rooting Habit—On flood plains, the balsam poplar root system is multilayered, owing to the deposition of new soil by periodic flooding. Although early root development is downward, subsequent development progresses upward as root development occurs on the buried stem. In one instance, major new root development occurred at least six times as the initial root system and 2 m (6.6 ft) of the main bole were buried by silt deposition during a 30- to 40-year period *(40)*. Root development on the buried stem of seedlings occurs within several weeks of burial and appears to be associated with the presence of preformed root primordia *(8,34)*.

Expansion of the root system and subsequent sucker production can play an important role in clone development and colonization of a site after the seedling ortet becomes established. Extension of lateral roots 1 to 3 cm (0.4 to 1.2 in) in diameter has been observed to be at least 14 m (46 ft) in 15-year-old clones. Expansion of the root system ranged between 0.5 and 8.0 m (1.6 and 26 ft) in a 15-year-old clone; maximum rate of expansion occurred between 5 and 9 years *(33)*. Root system expansion determined from clone size and age appears to be lower at treeline than at lower elevations where clones of about the same size occur but are 6 to 10 times older *(6,33,35)*.

On sites without active soil deposition, formation of the root system is predominantly downward and lateral. Depth of rooting is restricted on the relatively wet sites where balsam poplar is commonly found. Lateral root spread on upland sites is at least 8 to 12 m (26 to 39 ft).

Reaction to Competition—Balsam poplar shows all the characteristics of an early successional species: that is, low shade tolerance, rapid juvenile growth, prolific seed production, relatively short life span, good self-pruning, and replacement by more tolerant associates. It is most accurately classed as very intolerant of shade.

In primary succession on river flood plains, balsam poplar is an early invader and is associated with various willows and alder for about 20 years after formation *(53)*. It appears to assume dominance as a result of greater stature and relative growth rate than willow and alder, which precede it in succession, and white spruce, which follows it *(58,59)*. It may have an allelopathic effect on alder germination and germinant development, but these effects have not been substantiated under field conditions *(27,58,59)*. Balsam poplar bud extracts inhibit nitrification under laboratory conditions, indicating the potential for nitrogen conservation within poplar stands and an effect on forest development and succession *(49)*. It is the dominant species for about 50 years. White spruce gradually replaces balsam poplar, and by age 100 to 150 years, the poplar is a minor component of the stand. Deviations from this general pattern include the Yukon and Susitna Rivers where poplar stands more than 200 years old occur, and white spruce is a minor species present mainly in the understory.

Balsam poplar can be important in secondary succession on burns and cutovers or primary succession on lakeshores and sites severely disturbed by mining and construction. Asexual and sexual reproduction are important in burned and cutover areas, but only sexual reproduction is important on severely disturbed sites. Balsam poplar can reproduce asexually under stand conditions, but the suckers are short lived.

Damaging Agents—Susceptibility of balsam poplar to fire is determined by characteristics of individual trees and stands. Thickness of bark increases with age, giving increased resistance to fire; however, the bark of mature trees tends to be deeply fissured, and the protection afforded the cambium is less than if a continuous sheath surrounded it. Mature trees can withstand mild and perhaps moderately intense fires. Balsam poplar supports crown fires only under the severest burning conditions *(41)*.

Fire fuels differ in the various vegetation types where balsam poplar occurs. Pure stands of balsam poplar support fires of less intensity than those in mixed conifer-hardwood stands, and tree survival is greater. Early successional stands containing only hardwoods are less likely to burn intensely than later successional stages or mixed balsam poplar-conifer stands *(41)*. Balsam poplar produces root suckers after fire, and burned sites can be colonized by seed reproduction when mineral soil seedbeds are created.

As rivers create sites for establishment of balsam poplar, they also destroy sites with established stands. This process can be gradual as the river slowly undermines its bank at the rate of a few feet per year, or the erosion can be dramatic. It is not uncommon to see river channels change by 30 to 60 m (100 to 200 ft) in several years. These channel changes can destroy significant areas of established poplar stands.

Moose, deer, elk, and other animals browse on balsam poplar stem material but eat little foliage *(3)*. Stems as large as 5 cm (2 in) d.b.h. may be broken by moose and the tops browsed. Where browsing occurs for only 1 or 2 years, however, form is not adversely affected because subapical buds rapidly replace damaged terminals. Simulated browsing of 9- to 14-year-old poplars resulted in increased twig biomass, indicating that only under the severest, repeated browsing is it adversely affected *(16)*.

Resin of balsam poplar appears to repel snowshoe hares, and foliar buds have higher resin contents than internodes. As a result, hares may eat internodes of twigs and stems but not the buds *(3,38)*. High terpene and phenolic resin content are sufficient to reduce cellulose digestion, making balsam poplar less palatable to animals *(43)*.

Girdling by hares or rodents can kill saplings or small trees above the girdle, but dormant buds from below the girdle usually form a new stem. Ruffed grouse may feed on staminate buds in the winter.

Beaver frequently cut balsam poplar growing along watercourses; usually, sprouts are not produced or, if they are, they either die or are browsed and subsequently die. On small streams, ponds created by beaver dams can kill poplars growing in or adjacent to ponded areas.

The poplar and willow wood borer *(Cryptorhynchus lapathi)*, bronze poplar borer *(Agrilus liargus)*, and the poplar borer *(Saperda calcarata)* are among the most damaging insects. They girdle or badly weaken trees larger than 2.5 cm (1 in) in diameter by tunneling in the main stem and limbs *(9)*.

The forest tent caterpillar *(Malacosoma disstria)*, satin moth *(Stilpnotia salicis)*, gray willow leaf beetle *(Pyrrhalta decora decora)*, and aspen leaf beetle *(Chrysomela crotchi)* feed on balsam poplar foliage, but the species is not their principal host *(1)*. The highly resinous buds and leaves of balsam poplar may render them relatively less palatable than the principal tree hosts *(3)*.

In mature trees, the most common decay-causing fungal species is *Phellinus tremulae* with *Pholiota destruens*, *Corticium expallens*, and *Bjerkandra adusta* also being important. A canker caused by *Neofabraea populi* has been observed on balsam poplar in Ontario less than 3 cm (1.2 in) in diameter *(22,23)*. The occurrence of decay varies with site conditions and among clones, with the latter appearing to be the most important cause of resistance *(23)*. Infection by *Rhytidiella moroformis* causes a roughening of the normally smooth bark and the formation of deep furrows. *Melampsora* spp. cause a leaf rust and *Linospora* spp., a leaf blight *(22)*. *Venturia populina* causes a leaf and twig blight and can stunt the main stem.

Septoria musiva and *S. populicola* cause a leaf spot and canker on balsam poplar seedlings. *Septoria musiva* was reported to cause the highest percentage of canker and leaf spot in southern Manitoba. *Septoria* incidence on native poplars within their range is negligible *(61)*.

Frost damage occurs to trees of all ages in exposed stands established after burns and logging, in nursery stooling beds, and in plantations of hybrid poplar *(60)*. Entire twigs may be shed. Distortion from frost damage occurs adjacent to cankers, and dieback results in burl formation, bud proliferation, sucker production, and uneven development of bark, leaf, and sapwood *(60)*.

Special Uses

Natural stands are generally described as underutilized, but its use is increasing as hardwood utilization increases in the mixed-wood section of the boreal forest. Although the wood can be used for a variety of products (for example, pulp, veneer, core stock, boxes, crates, brackets), species such as aspen and cottonwood are preferred. Waferboard with excellent mechanical qualities can be produced from balsam poplar; however, special procedures are needed to efficiently waferize the wood *(17,42)*. In northern areas, balsam poplar is used for structural lumber and milled house logs when other species are not available.

Balsam poplar hybrids have a potential for a variety of uses. *Populus balsamifera* × *P. deltoides* (*Populus* × *jackii*) are used as windbreak and shelterwood plantings in the northern plains region. Other balsam poplar hybrids are being tested in short rotation, intensive culture plantations. When properly cultivated, irrigated, and fertilized, these hybrids yield about three or four times as much biomass as native aspen in northern Wisconsin. The resulting pulpwood is of acceptable quality. The foliage and small woody component can be converted to an animal feed supplement *(26,70)*.

Balsam poplar and its hybrids are used or have potential value in urban forestry and soil stabilization projects, particularly in the northern portion of the range and in the plains area of western Canada where the number of indigenous species available for these purposes is limited. In urban situations, however, balsam poplar has several undesirable traits. The branches of older trees tend to be brittle, female trees produce large amounts of residue from the spent catkins, and relatively rapid root suckering can result in unwanted colonization of lawns, sidewalks, and roadways.

Anyone that has ever walked into a poplar stand in the spring at bud break is impressed with the fragrance in the air. This fragrance comes from the volatile compounds in the buds and other parts of the tree. These compounds have been identified and may have useful biological and esthetic properties *(38)*. Various extracts from the winter buds of poplar were recognized by native peoples as having therapeutic value. For example, a salve or ointment (balm of Gilead) made by heating the winter buds in oil was used to relieve congestion *(52)*. In recent years, the bark has been collected and carved into figures that are sold in gift shops.

Genetics

Balsam poplar is in the section Tacamahaca of the genus *Populus* *(24)*. Two varieties have been identified: the typical variety *Populus balsamifera* var. *balsamifera* and *P. balsamifera* var. *subcordata*, found in eastern Canada *(2)*.

Balsam poplar and black cottonwood (*Populus trichocarpa*) have hybridized and produced mixed populations. Because of this intermixing, black cottonwood has been suggested as a subspecies (i.e., *Populus balsamifera* subsp. *trichocarpa*) *(2,37)*. Where balsam poplar and black cottonwood overlap, hybrids with a range of characters intermediate to those of the two species are found. An index using capsule shape, capsule pubescence, and carpel number has been developed *(2,55)*. Other hybrids have been reported between balsam poplar and *P. alba*, *P. laurifolia*, *P. nigra*, *P. simonii*, *P. suaveolens*, *P. tremula*, and *P. tristis* *(7,37,69)*.

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Populus deltoides Bartr. ex Marsh. **Eastern Cottonwood**

Salicaceae **Willow family**

P. deltoides Bartr. ex Marsh. var. deltoides
Eastern Cottonwood (typical)

D. T. Cooper

P. deltoides var. occidentalis Rydb.
Plains Cottonwood

David F. Van Haverbeke

Eastern cottonwood *(Populus deltoides)*, one of the largest eastern hardwoods, is short-lived but the fastest-growing commercial forest species in North America. It grows best on moist well-drained sands or silts near streams, often in pure stands. The lightweight, rather soft wood is used primarily for core stock in manufacturing furniture and for pulpwood. Eastern cottonwood is one of the few hardwood species that is planted and grown specifically for these purposes.

Besides the typical eastern variety (var. *deltoides*), there is a western variety, plains cottonwood (var. *occidentalis*). Its leaves, more broad than long, are slightly smaller and more coarsely toothed than the typical variety.

EASTERN COTTONWOOD

Eastern cottonwood (typical) *(Populus deltoides* var. *deltoides)* is also called southern cottonwood, Carolina poplar, eastern poplar, necklace poplar, and álamo.

Habitat

Native Range

Eastern cottonwood (figs. 1, 2) grows along streams and on bottom lands from southern Quebec westward into North Dakota and southwestern Manitoba, south to central Texas, and east to northwestern Florida and Georgia. The north–south distribution extends from latitude 28° N. to 46° N. It is absent from the higher Appalachian areas and from much of Florida and the Gulf Coast except along rivers. The western boundary is not well defined because eastern cottonwood intergrades with var. *occidentalis*, plains cottonwood, where the ranges overlap. Altitude is a primary determiner of the western boundary.

Climate

In various parts of its range, eastern cottonwood is subjected to temperatures as high as 46° C (115° F) and as low as -45° C (-50° F). Average January temperatures vary from -10° C (14° F) to 8° C (46° F). It occurs in areas with from less than 100 to more than 200 consecutive frost-free days per year. Rainfall ranges from less than 380 mm (15 in) in the northwest corner of the range to more than 1400 mm (55 in) in the southern part of the range. In the dryest parts of its range, eastern cottonwood receives most of its moisture from streams, making rainfall requirements meaningless. In the lower Mississippi Valley, more than one-third of the rain falls during the growing season, following a full subsoil recharge during the winter. Flooding often provides additional water. Nevertheless, there is usually inadequate moisture for optimum growth during the latter part of the growing season.

Soils and Topography

The species survives on deep, infertile sands and clays but makes its best growth on moist well-drained, fine sandy or silt loams close to streams. The soils of most cottonwood sites are in the soil orders Entisols and Inceptisols. The best sites are characterized by absence of mottles in the upper 46 cm (18 in), water tables from 60 to 180 cm (24 to 72 in), bulk density of less than 1.4 g/cm^3 (0.8 oz/in^3), pH of 5.5 to 7.5, and greater than 2 percent organic matter *(1)*. Sites frequently meet the requirements

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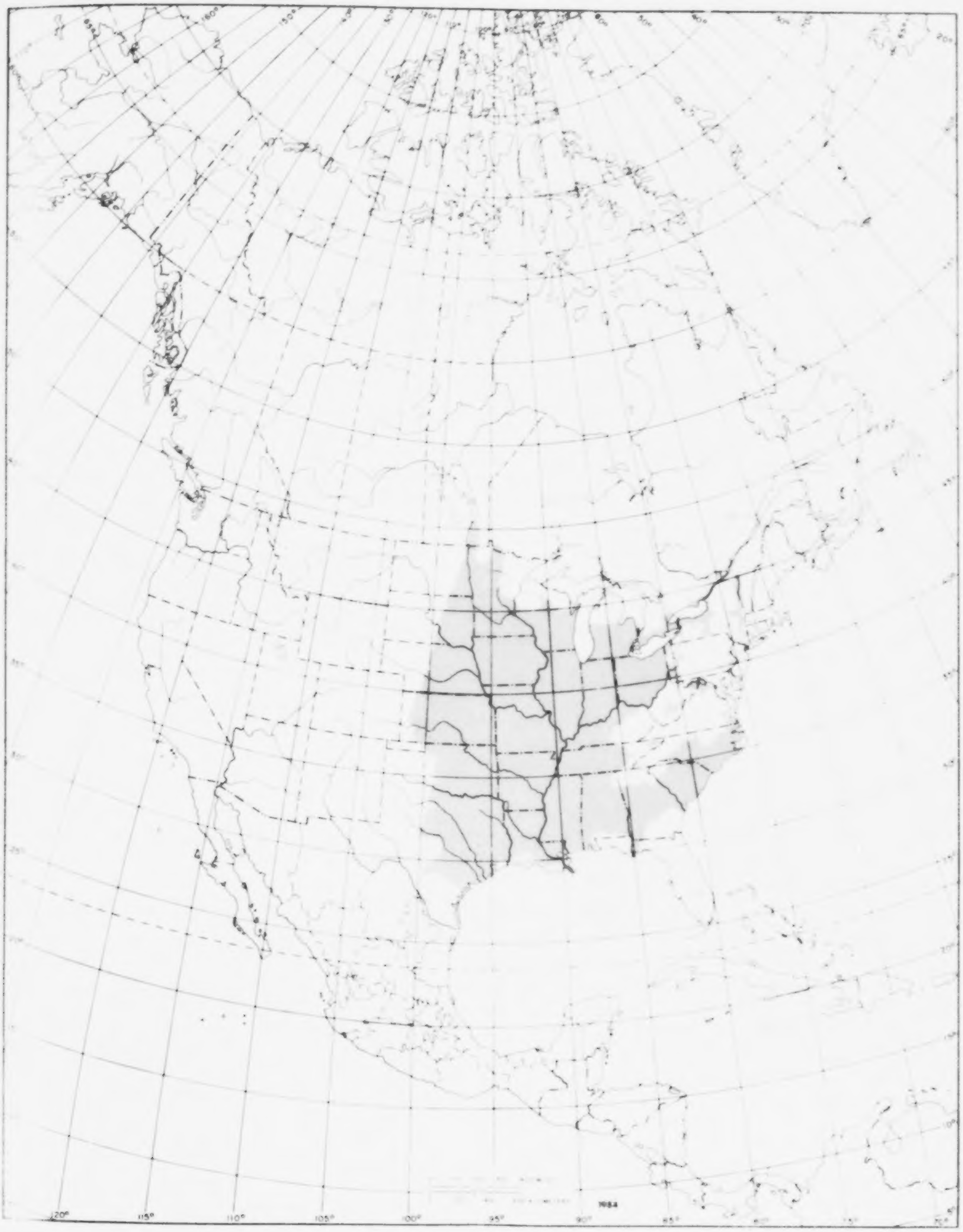
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Figure 1.—*The native range of eastern cottonwood.*

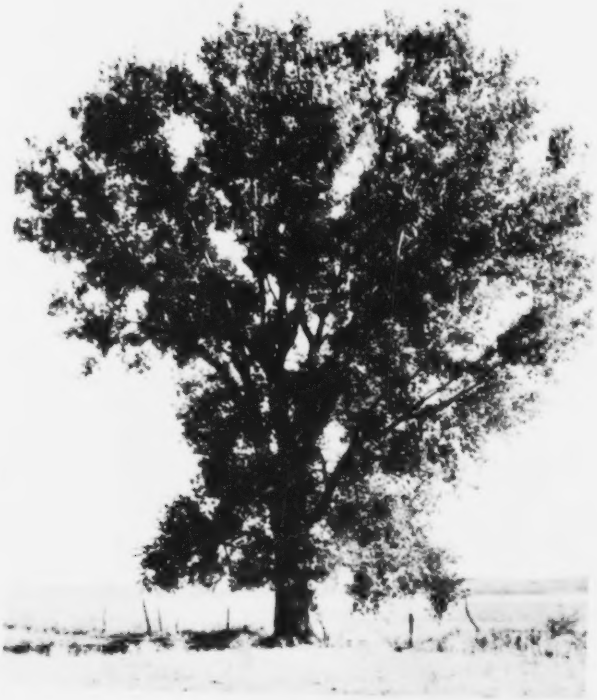

Figure 2—*Eastern cottonwood tree 20 m (65 ft) tall and 51 cm (20 in) in d.b.h.*

for good growth, but because of competition or lack of proper seeding conditions, planting is necessary for stand establishment.

Eastern cottonwood is not often found as a well-formed tree at an elevation of more than 4.6 to 6.1 m (15 to 20 ft) above the average level of streams. In the lower Mississippi River Valley, the best sites are in the batture, the land between the levees and the river. Here the species grows on the front land ridges, the high land or banks of present or former stream courses, on well-drained flats, the general terrain between low ridges, and rarely on abandoned fields on well-drained ridges in the first bottoms *(17)*. Where it occurs on slopes, it is confined to the lower ones that remain moist throughout the growing season. An example is the brown loam bluff area of loessial soil along the eastern side of the lower Mississippi River flood plain. Fine cottonwood specimens are frequent in the bottoms and on the lowest slopes bordering the small water-courses emerging from the bluffs.

Associated Forest Cover

Eastern cottonwood is the key species in the forest cover type Cottonwood (Society of American Foresters Type 63) and is an associate in the following types *(6)*: Black Ash–American Elm–Red Maple (Type 39), Bur Oak (Type 42), River Birch–Sycamore (Type 61), Silver Maple–American Elm (Type 62), Sweetgum–Willow Oak (Type 92), Sycamore–Sweetgum–American Elm (Type 94), and Black Willow (Type 95).

Other tree associates of eastern cottonwood are hackberry *(Celtis occidentalis)*, sugarberry *(C. laevigata)*, green ash *(Fraxinus pennsylvanica)*, box elder *(Acer negundo)*, river birch *(Betula nigra)*, white ash *(F. americana)*, slippery elm *(Ulmus rubra)*, blackgum *(Nyssa sylvatica)*, American hornbeam *(Carpinus caroliniana)*, and eastern hophornbeam *(Ostrya virginiana)*.

In the area where cottonwood attains its best development, roughleaf dogwood *(Cornus drummondii)* and swamp-privet *(Forestiera acuminata)* are major noncommercial tree and shrub associates.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Eastern cottonwood is dioecious. The sex ratio is about 1 to 1 *(8)*. Floral buds form in the summer prior to opening the next spring. Male buds develop somewhat earlier than female buds and are much larger. Flowering occurs from February to April before leaves appear. Male flowers are only 8 to 13 cm (3 to 5 in) long. They have 40 to 60 stamens and are reddish in color and more conspicuous than the female flowers. Female flowers elongate to 15 to 30 cm (6 to 12 in). Males tend to flower a few days earlier than females. Flowering varies by as much as a month among trees in a stand *(9)*. As a result, early-flowering trees do not have the opportunity to cross with late-flowering trees. Trees as young as 4 to 5 years old have flowered. Northern trees flower at lower temperatures than do southern trees. Seeds develop 30 to 60 per capsule on short stalks on long catkins. Each capsule has 3 or 4 valves.

Seed Production and Dissemination—Seed production starts when the trees are 5 to 10 years old, increasing rapidly in amount as the trees become older and larger. Estimates of annual seed production of a single open-grown tree have been as high as 48 million seeds *(3)*. Good seed crops are the rule. About 35 liters (1 bushel) of fresh fruit yields 1 kg (2.2 lb) of seeds, or about 770,000 cleaned seeds *(19)*.

Seed dispersal follows flowering by about 2 months in southern populations and a somewhat shorter period in the North. It is characterized by considerable variation among trees as well as a lengthy dispersal period for some individual trees *(9)*. Seed dispersal occurs from May through mid-July in the South and June through mid-July in the North *(19)*. The dispersal pattern results in abundant deposits of seeds along water courses as spring flood waters recede. Seeds may be carried several hundred feet by the wind, aided by the "cotton" attached to the seed. Seeds falling in water may be carried a long distance from the parent tree before being left on silt deposits.

Seedling Development—Unless floating on or immersed in water, cottonwood seeds must reach a favorable seedbed and germinate very soon after falling. Germination of fresh seeds may exceed 90 percent. Seedlings are delicate for the first few weeks. Rains, very hot sunshine, and damping-off fungi kill many of them. Very moist, exposed mineral soils, such as fresh silt deposits, are required. Germination is epigeal. Growth rate of the fragile seedlings is slow for the first 3 weeks but may be very rapid after that. Full sunlight for a substantial part of each day is required after the first few weeks.

Fully mature seeds that are dried promptly to 5 to 8 percent moisture and stored at temperatures just above freezing maintain viability for several months. Storage at -20° C (-4° F) may prolong viability for 5 or more years *(20)*. It is best to increase the moisture content gradually when attempting to germinate very dry seed.

Vegetative Reproduction—Satisfactory sprouting has occurred on low-cut stumps of trees as old as 25 years of age *(22)*. Reproduction by root suckers is not common. Artificial propagation of the species normally involves use of cuttings from 1-year stem growth from nursery trees *(23)*. These may or may not be rooted before outplanting.

The planting season in the North is short, coinciding with the beginning of the growing season. Rooted cuttings commonly are used under these conditions.

In the Southern United States, unrooted cuttings 30 to 50 cm (12 to 20 in) long provide a satisfactory, economical means of planting *(15)*. Survival rates of 70 to 90 percent are normally achieved, depending on the genetics of the clones, quality of cuttings, and field conditions. Root-inducing hormones normally are not used. Rooted or unrooted long cuttings are sometimes used to reach moisture, to reduce damage from deer, to permit less intensive site preparation, and to provide greater flood tolerance. Because operational use of asexual propagation of cottonwood permits immediate and complete utilization of superior genotypes, rooting ability is of great importance.

Propagation from 1-year-old wood from older trees is often difficult, but some success is usually achieved. Repropagation from the resulting material is often satisfactory. Clones tracing back to older trees normally have the smooth, somewhat thin, bark characteristics of the tops of older trees.

Sapling and Pole Stages to Maturity

Growth and Yield—Eastern cottonwood is one of the tallest species east of the Rocky Mountains. Heights of 53 to 58 m (175 to 190 ft) and diameters of 120 to 180 cm (48 to 72 in) have been reported *(17)*, as have age 35 stand volumes exceeding 420.0 m^3/ha (30,000 fbm/acre) of sawed lumber *(5, 10, 14, 22)*.

The most phenomenal growth has been from trees planted on favorable sites in the South and receiving adequate weed control. Scientists have recorded heights of 13 m (43 ft) at age 3 and more than 30 m (100 ft) at age 9 on individual trees. In one plantation, unpruned trees at wide spacing averaged 29 cm (11.4 in) d.b.h. at age 5 *(11)*. The best yields with close spacing of unimproved clones without irrigation in the South has been about 138.6 m^3/ha (1,980 ft^3/acre) total volume at age 4 with 2,700 stems per hectare (1,100/acre) *(21)*.

Rooting Habit—Root growth of new seedlings is so slow that the plants are easily dislodged by rain droplets. After the first 3 weeks, root growth accelerates and lateral root growth may exceed height growth for the first year. Most of the roots are in the uppermost, best aerated layer of soil *(2)*. They are nearer the surface in clay soils than in loam soils. Following siltation, roots develop on the covered portion of the stem. Cottonwood trees planted from conventional 20 to 60 cm (8 to 24 in) cuttings have fewer deep roots and are not as well anchored against root lodging as those established naturally or as deep-planted seedlings or rooted cuttings.

Reaction to Competition—Cottonwood is classed as very intolerant of shade. It is more intolerant of shade than any of its associates except willow. Although the two frequently seed in together, pure stands of one or the other are the general rule after the first few years. Willow survives on the wetter sites and cottonwood on the slightly higher, drier sites. Its faster growth allows cottonwood to crowd out the willow except where prolonged deep flooding drowns the cottonwood component of the stand.

Cottonwood responds poorly to release following crowding. Only those trees with the best crowns respond. In natural stands, uneven spacing and size permit some trees to become dominant, and natural thinning allows production of large trees. Under plantation conditions and particularly when only clones with similar growth rates are used and all trees get off to a good start, stagnation can occur quickly. Spacing and timing of thinning become critical under these conditions. Optimum growth of individual trees requires very wide, seemingly wasteful, spacing. On the best sites in the South, cottonwood planted initially at a spacing of 3.7 by 3.7 m (12 by 12 ft) should be thinned by removing half of the trees at age 3 and again at age 5 if rapid growth rate of individual trees is to be maintained.

Damaging Agents—Although cottonwood grows rapidly under ideal conditions, numerous agents can disrupt its schedule and cause death or loss in tree quality or growth rate. These include insects, disease organisms, flood, fire, and various animals. At least 10 insect species and 12 diseases cause major damage to eastern cottonwood throughout its range *(16)*.

A clearwing borer, *Paranthrene dollii dollii*, attacks the lower stem. Another clearwing borer, *P. tabaniformis*, attacks terminals and small branches causing breakage of terminals. The poplar borer, *Saperda calcarata*, attacks trunks of trees 3 or more years old and may riddle portions of the trunks with tunnels, causing serious degrade or breakage. The cottonwood borer, *Plectrodera scalator*, attacks the root collar and roots of both large and small trees. Small, closely-spaced trees break off easily from this damage. The cottonwood twig borer, *Gypsonoma haimbachiana*, causes stunting, forking, and other malformations in young cottonwood. The cottonwood leaf beetle, *Chrysomela scripta*, defoliates and kills terminals, producing forked stems. The poplar tentmaker, *Ichthyura inclusa*, can cause repeated defoliation, resulting in mortality.

Numerous disease organisms attack cottonwood. *Septoria musiva* causes a small canker that opens a path for other canker organisms. *Cytospora chrysosperma* causes a canker where sites are adverse and tree vigor is low. *Fusarium solani* enters wounds, particularly after major floods, to cause a canker. Two other canker-producing organisms are *Phomopsis macrospora* and *Botryodiplodia theobromae*. On vigorous trees, cankers usually callus over. *Melampsora medusae* causes leaf rust which results in premature defoliation and reduced growth rate. *Marssonina brunnea* causes a leaf spot that also results in early defoliation. *Septoria musiva*, in addition to causing a canker, causes a leaf spot. New leaves may be infected from old leaves or cankers.

Since cottonwood grows primarily in relatively low areas near streams it is subjected to frequent flooding. Floods during the dormant season or floods of short duration during the growing season may benefit cottonwood trees by fully recharging subsoil moisture and providing some degree of vegetation control. Floods that overtop newly sprouting cuttings or established trees for prolonged periods during the growing season or that result in stagnant water pools are harmful.

Cottonwood of all ages is very susceptible to fire. A very light burn kills younger trees, while burns of greater intensity kill or wound larger ones. Butt rot, a common result of fire injury, is uncommon in cottonwood, however *(13)*.

Seedlings and young trees are browsed by rabbits, deer, and domestic stock. A substantial portion of the trees can recover from this damage. Beavers cut sapling and pole-size trees for food and for dam construction. The resulting ponds may drown cottonwood trees.

Special Uses

Eastern cottonwood is frequently planted to give quick shade near homes. Male clones, which have none of the objectionable "cotton" associated with seed, are preferred. Windbreaks are occasionally established with cottonwood as a component. Cottonwood is suitable for soil stabilization where soil and moisture conditions are adequate, as along stream or ditch banks. Deep planting permits reforesting of nonproductive fields with sandy soils having available moisture beneath a dry surface layer.

There has been considerable interest in cottonwood for energy biomass, because of its high yield potential and coppicing ability. There has also been interest in growing it for inclusion in cattle feed, since it is a good source of cellulose relatively free of undesirable components, such as tannins. The new growth is high in protein and minerals.

Genetics

Population Differences

Eastern cottonwood tends to be linearly distributed along streams. Differences in climate, soils, day length, and exposure to pests result in genetic differences among these populations. Gene flow to downstream portions of the population may occur as a result of seeds floating in the current. The cottonwood in the lower reaches of the Mississippi River may contain genes from many tributaries.

Races and Hybrids

Some scientists recognize three subspecies of eastern cottonwood *(7)*. These include *angulata*, a southern strain, *missouriensis*, a central or intermediate strain, and *monilifera*, a northern strain. These divisions are based upon minor differences in morphological traits. Plains cottonwood *(Populus deltoides* var. *occidentalis)*, discussed in the next paper, appears to be a legitimate race or subspecies, growing at higher altitudes under more adverse conditions.

Eastern cottonwood hybridizes freely with plains cottonwood and crosses with several other species either naturally or artificially. It is most noted for its excellent hybrids with *Populus nigra*. Hybrid swarms with *P. balsamifera*, *P. tremuloides*, and *P. grandidentata* are reported *(18)*, as well as natural hybrids with *P. trichocarpa (4)*. The following natural interspecific hybrids are recognized *(12)*:

Populus × *acuminata* Rydb. *(P. angustifolia* × *deltoides)*

Populus × *bernardii* Boivin *(P. deltoides* × *tremuloides)*

Populus × *jackii* Sarg. *(P. balsamifera* × *deltoides)*

Populus × *polygonifolia* Bernard *(P. balsamifera* × *deltoides* × *tremuloides)*

In addition, many hybrids between eastern cottonwood and other poplars have been produced artificially.

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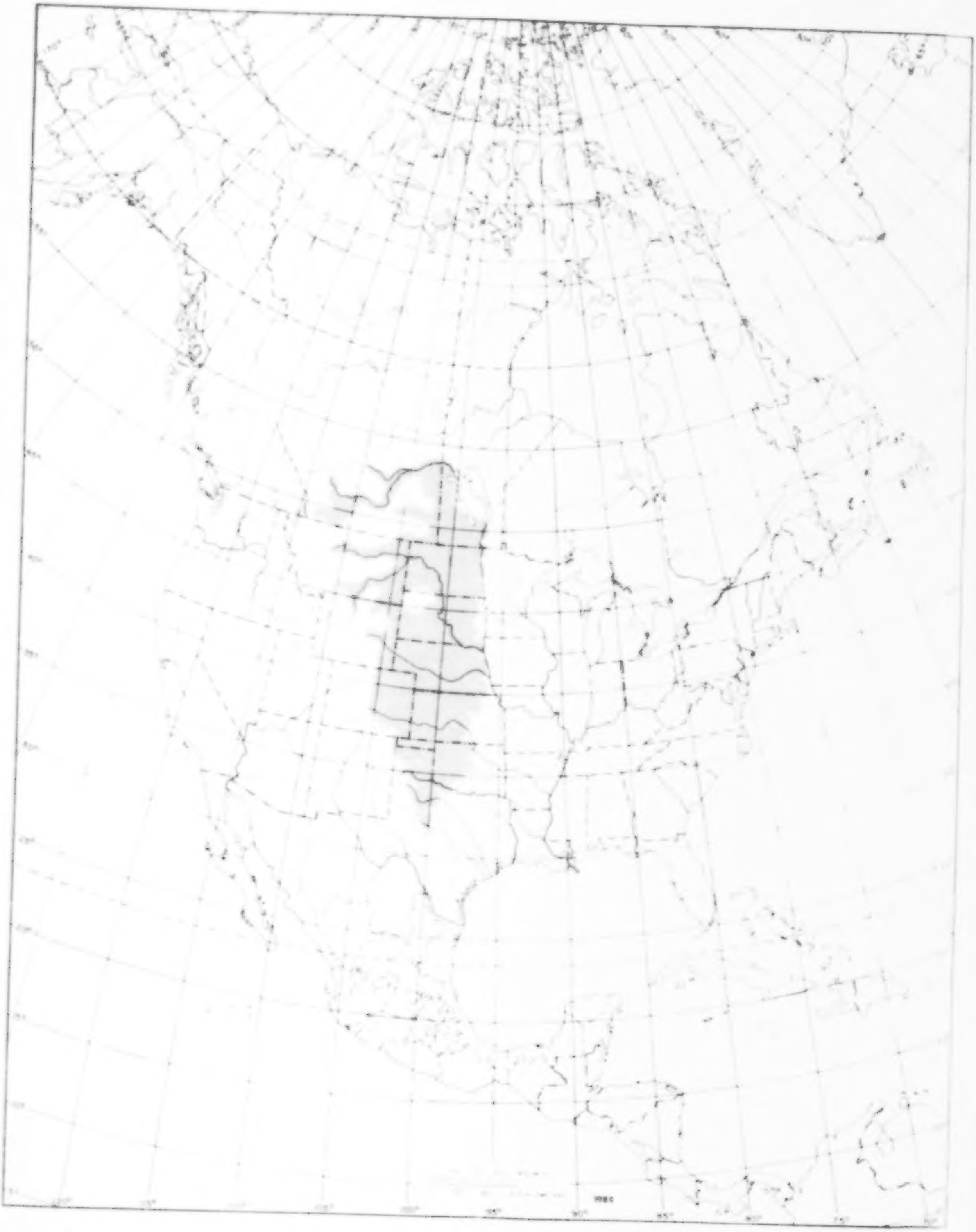
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Figure 3—*The native range of plains cottonwood.*

23. Zsuffa, L. 1976. Vegetative propagation of cottonwood by rooting cuttings. *In* Proceedings, Symposium on Eastern Cottonwood and Related Species. Sept. 28–Oct. 2, 1976. Greenville, MS. p.99–108. Bart A. Thielges and Samuel B. Land, Jr., eds. Southern Forest Experiment Station, New Orleans, LA.

PLAINS COTTONWOOD

Plains cottonwood (*Populus deltoides* var. *occidentalis*) also has other common names with geographical and topographical connotations: Texas cottonwood, river cottonwood, western cottonwood, and plains poplar.

Habitat

Native Range

The range of plains cottonwood (fig. 3) encompasses a broad, irregular-shaped band approximately 800 km (500 mi) wide and 2400 km (1,500 mi) long, extending south southeasterly from the southern prairie provinces of Canada into the high plains of northern Texas. This range spans approximately 20° in longitude (92° to 115° W.) and 25° in latitude (30° to 55° N.) (*14,19*).

Specifically, plains cottonwood grows from southern Alberta, central Saskatchewan, and southwestern Manitoba in Canada, south through the Great Plains in North Dakota, South Dakota, Nebraska, Kansas, western Oklahoma into north–central Texas and extreme northeastern New Mexico; north in Colorado, eastern Wyoming, and eastern Montana. The eastern limit of the range is not well defined because it integrades with the western limit of the range of the typical variety, eastern cottonwood (var. *deltoides*) (*13,14*).

Climate

The climate of the Great Plains, the region in which plains cottonwood grows, is distinctly continental. The region is characterized as dry subhumid to semiarid, with extremes and rapid fluctuations in temperature, unpredictable and limited precipitation, frequent and cyclic droughts, and strong persistent winds (*3*).

Average annual precipitation varies from about 250 mm (10 in) in the northern and western Great Plains to about 760 mm (30 in) in the extreme southeastern part of the species range. About 75 percent of the annual precipitation occurs during the growing season. Drought periods of 35 to 60 consecutive days may be expected annually, and periods of 60 to 70 days without rainfall may occur once in 10 years. Infrequent drought periods of 90 to 120 days have been recorded in the northern and southern plains, respectively. Drought hazard is greatest in the autumn and winter in the northern plains, and in the winter in the southern Great Plains where snowfall is less. High-velocity winds occur in all seasons but are strongest and most persistent during winter and early spring (*29*).

Average January temperatures vary from −15° C (5° F) in the North to 4° C (40° F) in the South. Minimum temperatures range from −46° C (−50° F) in the north to −18° C (0° F) in the South, with maximum temperatures of 38° C (100° F) to 46° C (115° F) throughout the region. The frost-free period varies from 100 days in the North to 220 days in the south (*29*).

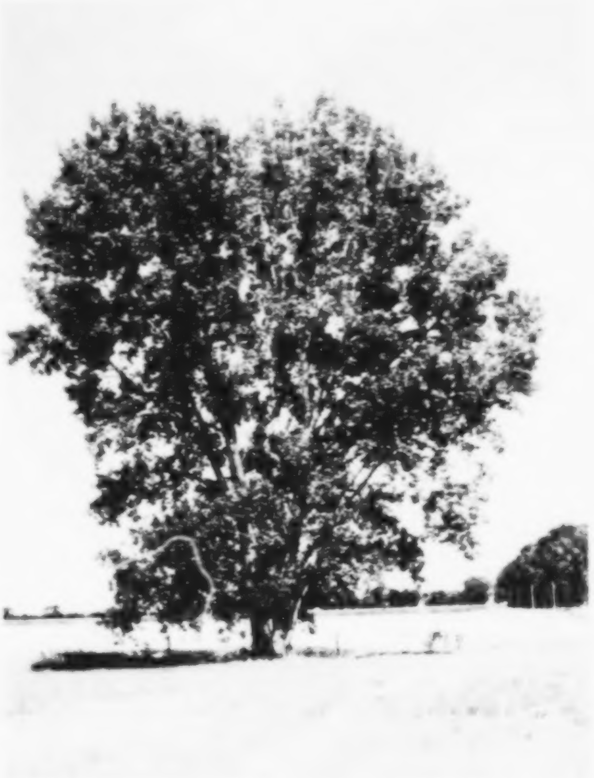

Figure 4—*Plains cottonwood as often seen on the prairies of the Great Plains.*

Soils and Topography

Plains cottonwood grows along most of the rivers and streams that flow through the loessial soils of the Great Plains on sites that are 2.4 to 3.7 m (8 to 12 ft) above the water table. The taxon predominates on the level, narrow stringers of the river floodplains and stream bottom lands that cross the region. It is common in pure stands on river sandbars and on overflow land in the bends of large rivers but is also found in the beds of intermittent streams *(1)*.

Plains cottonwood grows on soils of the order Entisols, mainly along alluvial streams, and on soils of the orders Mollisols, Alfisols, and Inceptisols on stream terraces, in drainage ways, and in bottom lands and subirrigated valleys. Best development is on deep, rich, well-drained loams; however, the species also grows on level subirrigated uplands of deep, sandy soils *(1)* (fig.4). Soil texture and fertility seem to be of lesser importance than moisture, however, in determining its occurrence.

Plains cottonwood grows between elevations of about 300 m (1,000 ft) near its eastern limit to about 1830 m (6,000 ft) in the foothills of the Rocky Mountains. It is seldom found above 2130 m (7,000 ft) *(27)*.

Associated Forest Cover

Plains cottonwood can grow in pure stands, but it is frequently found as an associate in three forest cover types: Bur Oak (Society of American Foresters Type 42), Cottonwood (Type 63), and Cottonwood-Willow (Type 235) *(22)*. Black willow *(Salix nigra)* and peachleaf willow *(S. amygdaloides)* are the most common associates. Other associates on the better sites include American elm *(Ulmus americana)*, slippery elm *(U. rubra)*, hackberry *(Celtis occidentalis)*, boxelder *(Acer negundo)*, green ash *(Fraxinus pennsylvanica)*, red mulberry *(Morus rubra)*, black walnut *(Juglans nigra)*, American sycamore *(Platanus occidentalis)*, eastern redcedar *(Juniperus virginiana)*, and silver maple *(Acer saccharinum)* *(1,17,30)*.

Associated shrubs and vines include sandbar willow *(S. exigua)*, red-osier dogwood *(Cornus stolonifera)*, indigobush *(Amorpha fruticosa)*, coralberry *(Symphoricarpos orbiculatus)*, wild grape *(Vitis* spp.), poison-ivy *(Toxicodendron radicans)*, smooth sumac *(Rhus glabra)*, and American plum *(Prunus americana)*. In the western Plains, shrubs are scarce in the cottonwood stands, and several species of grasses and forbs are found in their place. These include sand dropseed *(Sporobolus cryptandrus)*, buffalograss *(Buchloe dactyloides)*, sunflowers *(Helianthus* spp.), lambs-quarters *(Chenopodium album)*, and Russian-thistle *(Salsola pestifer)* *(1)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Plains cottonwood is dioecious with only occasional deviations. Staminate and pistillate flowers are borne on twigs of the previous year's growth, appearing in early spring (April and May) before the leaves develop *(20,27)*. Pollination is by wind. Following anthesis, the staminate catkins dry and fall within 2 weeks. Four to 6 weeks, ranging from June through August, are required for seed maturation *(9,20)*.

The flowering period seems to be regular within the limits of geographic zones, but differences can occur in time of anthesis between stands and among trees within stands. Differences in date of flowering from year to year apparently depend upon temperatures. The ratio of staminate to ovulate trees is believed to be about 1 to 1. In the lower Mississippi Valley the ratio was reported to be 54 to 46 percent *(10)*.

Seed Production and Dissemination—Minimum seed-bearing age of plains cottonwood is about 10 years, and fair to large seed crops can be expected annually. The seeds are very small, yet relatively large for the genus; they range from 551,000 to 1,056,000 seeds per kilogram (250,000 to 479,000 lb). Seeds have a tuft of "cottonlike" hairs attached and are dispersed primarily by wind, but also by water, over long distances a few days after ripening. Seedfall among trees within a locality varies greatly and may extend for 6 weeks or longer *(9,20)*.

Seedling Development—The viability of fresh seeds is high; 98 percent germination has been attained during the first 5 days following dispersal *(9,20)*. Longevity of poplar seeds under natural conditions has been reported to be 2 weeks to 1 month. Vitality of fresh, unstored seed drops rapidly, however, if they are not kept moist. There is no evident dormancy.

Poplar seeds can be stored successfully and viability is prolonged if the moisture content is reduced to 4 or 5 percent. Air-dried *P. deltoides* seeds, stored in sealed containers at 1° to 4° C (34° to 39° F), were 100 percent viable after 6 months *(9,20)*. Seeds of some poplar species have been similarly stored in vacuum-packed jars at 0° C (32° F) for as long as 3 years *(11)*. Recently, it was demonstrated that *P. deltoides* seed stored at –20° C (– 4° F), either at normal air pressure or under vacuum, showed significantly higher germination than the same seed stored at 5° C (41° F) under vacuum (in sealed containers), after 6 months of storage. Thereafter, germination at -20° C (-4° F) remained unchanged during a 6-year study period, whereas germination of seed stored at 5° C (41° F) was considered unsatisfactory after 3.5 years. Eastern cottonwood seed should always be stored at below freezing temperature, even for short-term storage *(28)*. Germination is epigeal.

Plains cottonwood seed germinates within 48 hours after dispersal on proven mediums such as moist silt, sand, or fine gravel in full sunlight. The aboveground portion of the seedling develops rapidly and vigorously. Constant moisture is required for at least several weeks to ensure the establishment and survival of the slower developing root systems of the seedlings *(5,9)*.

The best planting sites are moderately well-drained, permeable, and fertile deep loam soils on bottom lands. Very sandy soil is suitable if the water table is within 3.7 to 4.6 m (12 to 15 ft) of the surface. Even upland sites are satisfactory if they are fertile, not too shallow, and if rainfall is abundant and well-distributed. Full sunlight, freedom from competition of weeds and grass (particularly sod), and abundant moisture throughout at least the first growing season are essential to seedling survival and establishment *(27)*.

Although initial establishment is usually good and growth is rapid on coarse sands and gravels of river bottom lands, periods of drought and fluctuating water tables make subsequent development uncertain *(17)*. Establishment of plains cottonwood on meander lobes of rivers in southern Canada is positively correlated with flood flows during seed dispersal (June 1–July 10) *(2)*. Floods during the seed-dispersal period recur in southern Alberta and northern Montana about every 5 years.

Vegetative Reproduction—Plains cottonwood is easily reproduced by stem cuttings from 1-year-old "ripened" wood. Since this species, like other members of the genus, sprouts vigorously from both roots and stumps of young trees, clonal "stool" beds are commonly established for the production of these cuttings. Cuttings can also be taken from pollards, 1-year-old plants, or epicormic branches of old plants *(11)*.

Healthy, straight, lignified wands without bark injuries approximately 2 m (6.6 ft) long and 3 to 30 mm (0.1 to 1.2 in) in diameter are cut from stool beds with a sharp knife during the dormant season (October to March), treated with fungicide, and placed in cool 5° C (41° F), moist storage *(11)*. The wands are divided into cuttings approximately 25.4 cm (10 in) long and 10 to 20 mm (0.4 to 0.8 in) in diameter at midpoint and inserted in a mist-sprayed greenhouse rooting bench containing moist sand as a medium.

Recent greenhouse and field tests in Nebraska demonstrated that cuttings taken from the basal end of wands produce significantly more roots than those taken from the upper portion. Also, cuttings from clones of Nebraska and Minnesota–Wisconsin origins produced significantly higher numbers of roots than those of other geographic sources *(33)*. About 4 to 6 weeks are required for rooting and subsequent field establishment. Rooted cuttings of *P. deltoides* are not root-pruned when field-planted.

Figure 5—Plains cottonwood on an upland, sandy, subirrigated Great Plains site in Nebraska.

Unrooted cuttings can also be field-planted. In wetter climates and in heavier soils, 25.4 cm (10 in) cuttings are satisfactory. In drier climates and in sandy soils, cuttings 50 to 80 cm (20 to 31 in) long have been more successful. In both situations, dormant cuttings are planted in the early spring and are completely buried except for the top bud and 3 to 5 cm (1 to 2 in) of the wand. Difficult-to-root clones can also be grafted *(11)*.

Experiments in Utah have shown that *Populus deltoides* (of unknown, but presumed eastern origin), *P. balsamifera*, and *P. angustifolia*, as well as *P. tremuloides*, produce abundant shoots (suckers) and roots from root cuttings (segments). New shoots and roots originate from pre-existing suppressed buds embedded in the periderm along the surface of the root cutting and from the region of the exposed cambium at the cut ends. The presence of lateral roots increased shoot growth, and the development of shoots and lateral roots responded to the inherent polarity of the root segments *(18)*. The probability that the closely related plains cottonwood will react similarly would seem to be high.

Sapling and Pole Stages to Maturity

Growth and Yield—Young plains cottonwood trees grow 1.8 to 3.7 m (6 to 12 ft) per year in height under favorable conditions, surpassing other native species of the Great Plains region in height and diameter growth. Growth is most rapid in the first 25 to 30 years, by which time the trees can reach 15.2 to 22.9 m (50 to 75 ft) in height and 61.0 to 91.4 cm (24 to 36 in) in diameter. Cottonwood sources from Missouri *(P. deltoides)* and Nebraska (Siouxland), along with silver maple (Acer saccharinum), ranked highest among seven species tested for the production of biomass during a 2-year study in Kansas *(12)*.

Plains cottonwood usually attains maximum development in about 40 to 50 years. Mature trees can be 24.4 to 27.4 m (80 to 90 ft) tall, with diameters of 1.8 to 2.4 m (6 to 8 ft), and with clear boles for 9.1 m (30 ft) or more. The trees are usually single-stemmed with an open, spreading, symmetrical crown of massive horizontal branches and stout, more or less angled branchlets and twigs (fig. 5). While plains cottonwood is relatively short-lived, it can remain vigorous for 80 to 90 years under favorable conditions *(21,27)*.

Survival and growth of cottonwoods on the Great Plains is directly dependent upon availability of moisture. Mortality during the drought of the mid-1930's was 59 percent along intermittent streams, 55 percent near springs that failed during the drought, and only 6 percent along continuously flowing streams *(1)*.

Fully stocked cottonwood stands along creek and river channels and overflow land in Kansas are estimated to yield 168.0 to 210.0 m^3/ha (12,000 to 15,000 fbm/acre) at 25 to 30 years of age *(21)*. In North Dakota, 30-and 50-year-old plantation yields were 59.5 to 219.8 m^3/ha (4,250 and 17,500 fbm/acre) gross merchantable volume, respectively, Scribner log rule *(26)*.

Plains cottonwood 94 cm (37 in) in diameter outside bark and 19.8 to 22.9 m (65 to 75 ft) tall, growing in the South Platte River bottom, Morgan County in eastern Colorado, attained gross volumes of 8.0 m^3 (283 ft^3) inside bark *(8)*. One could expect trees growing on more fertile and wetter sites along the Platte and Missouri River bottom lands in the eastern part of the range to achieve volumes in the magnitude of 11.3 m^3 (400 ft^3).

Rooting Habit—Early diameter and height growth of plains cottonwood surpasses that of other species native to the Great Plains region *(17)*. Growth and penetration of poplar seedling roots immediately following germination is reported to be relatively slow, however. About 5 days are required after germination for the primary root to begin downward growth, and after 12 days the root may be only 1.5 mm (0.06 in) long *(19)*. Growth continues slowly for 3 weeks to 1 month, at which time taproots of the cultivar Petrowskyana, for example, grown indoors in fairly strong light, averaged only 2.5 cm (1 in) in length at the end of 1 month. This growth pattern explains the critical need for continuous moisture during the seedling stage. Subsequent root growth is much more rapid.

Ninety-eight percent of the roots of a 43-year-old northern cottonwood *(Populus monilifera)*, 19.8 m (65 ft) tall, were found to be in the top 1.2 m (4 ft) of a prairie clay soil near Fargo, ND *(31)*. Roots of this and other non-drought-tolerant species formed shallow roots on dry sandy sites but had a tendency to grow deep vertical roots on very moist (nonsaturated) sandy sites. Similar trends of root development were revealed in excavations of plains cottonwood trees growing in silty loam soils in eastern Nebraska, where (1) a 14-year-old tree, 18.3 m (60 ft) tall, developed only shallow, widespread, and fibrous roots over and down to a water table 0.8 m (2.5 ft) deep; (2) a 16-year-old tree, 11.3 m (37 ft) tall, developed a moderately heavy root system downward to a water table 4.3 m (14 ft) deep and then branched outward; and (3) a 49-year-old tree, 21.3 m (70 ft) tall, developed a distinct and heavy taprooted pattern over an unreachable water table 18.3 m (60 ft) deep *(24)*.

Reaction to Competition—Plains cottonwood requires full sunlight for maximum growth. It is classed as very intolerant of shade and intolerant of root competition *(21)*. It grows either in pure stands, which thin naturally and rapidly, or in open mixed stands, both of which are nearly always even-aged *(17)*. After pioneering on alluvial sites, often with the willows, it is gradually replaced with other broadleaf species that can then become established under the forest conditions so created. Cottonwood does not normally regenerate until the overstory has broken up.

Damaging Agents—Prolonged periods of severe environmental stress, such as drought, weaken trees physiologically and increase their susceptibility to disease and insect pathogens. Plains cottonwood, with its high water requirement is especially vulnerable (1). *P. deltoides* var. *occidentalis* trees, considered water-tolerant, showed 47 percent high stress rate and 18 percent mortality when inundated late in the growing season in the Central Plains *(15)*.

Leaf rusts and stem cankers are the most widespread and damaging diseases. Leaf rusts cause premature defoliation of trees. This defoliation not only causes growth losses; it weakens the trees and increases their susceptibility to infection by other pathogens, which cause cankers and mortality.

Melampsora leaf rust caused by *Melampsora medusae* is one of the most serious leaf diseases of plains cottonwood. Others include Septoria leaf spot, caused by *Septoria musiva*, *Marssonina brunnea* leaf spot, and Alternaria leaf and stem blight, caused by *Alternaria tenuis (16)*.

The most serious of the canker pathogens is Cytospora canker *(Cytospora chrysosperma)*, which often results in wind-breakage at the wound area. Other canker pathogens include those caused by *Septoria musiva*, *Fusarium solani*, *Phomopsis macrospora*, *Botryodiplodia theobromae*, *Cryptosphaeria populina*, and *Pleurotus ostreatus*. Root and butt rots may be due to *Ganoderma lucidum Armillaria tabescens*, and *Scytinostroma galactinium (16)*.

The insects most damaging to plains cottonwood are the defoliators and wood borers; the former cause loss of vigor, the latter reduce the quality of lumber. Some of the more important defoliating insects include the cottonwood leaf beetle *(Chrysomela scripta)*, cottonwood dagger moth *(Acronicta lepusculina)*, forest tent caterpillar *(Malacosoma disstria)*, poplar leaffolding sawfly *(Phyllocolpa bozemani)*, fall cankerworm *(Alsophila pometaria)*, and the fall webworm *(Hyphantria cunea) (25)*.

Important boring insects include the poplar borer *(Saperda calcarata)*, cottonwood borer *(Plectrodera scalator)*, flatheaded wood borer *(Dicerca divaricata)*, carpenterworm *(Prionoxystus robiniae)*, poplar-and-willow borer *(Cryptorhynchus lapathi)*, and the bronze poplar borer *(Agrilus liragus) (25)*.

Several species of mites and aphids infest plains cottonwood, but their effects are not usually fatal.

Special Uses

Plains cottonwood is an important component of windbreak plantings in the Great Plains. It is frequently used as an ornamental to provide quick, if rather temporary, esthetic and protective effects. Plains cottonwood can produce an effective windbarrier 12.2 to 15.2 m (40 to 50 ft) tall in 15 to 20 years on stream lowlands and on deep, sandy, subirrigated lands *(17)*.

The wood of plains cottonwood is coarse, odorless, soft, and lightweight, yet relatively strong. The heartwood is pale yellowish brown, the sapwood nearly white. The wood frequently warps on drying and is not durable in contact with soil and other moist conditions. It nails without splitting, is clean appearing, and takes printing and stenciling well.

The wood is used primarily for pallets, rough construction lumber (farm buildings), interior parts of furniture, excelsior, crating, and wood pulp *(21,27)*. The pulp produces a very high-grade gloss paper.

New and potentially important commercial uses of the wood include roughage food for livestock and the production of fiber and reconstituted wood products derived from short-rotation (2- to 8-year) biomass operations *(6,23)*.

Genetics

Races

Within the large and climatically diverse north–south range of plains cottonwood, subtle but recognizable differences in the population have evolved by natural selection. What is here called *Populus deltoides* var. *occidentalis* has received at least nine names denoting either specific or varietal rank over the past two centuries *(14)*.

Recently, the eastern cottonwood *(Populus deltoides)* complex has been treated as a group of three intergrading subspecies showing random or clinal variation or both within each subspecies *(7)*. Plains cottonwood, on the basis of taxonomic affinities to the poplars of the Great Lakes region, was recognized as *P. deltoides* ssp. *monilifera* (Ait.) Eckenwalder. This treatment, supported by recent provenance evaluations in Nebraska, seems to be a more tenable interpretation. In these provenance evaluations, the poplars of Kansas, Nebraska, and South Dakota, with smooth bark, small branches, small leaves with a few or no glands and few serrations, and prolific rooting habit tended to be similar to poplars of Minnesota and Wisconsin origin *(32)*.

Hybrids

The eastern members of plains cottonwood *(Populus deltoides* var. *occidentalis)* intergrade with western-most eastern cottonwoods *(P. deltoides* var. *deltoides)*; therefore, the literature reveals no named hybrids between these very closely related populations *(14)*.

Interspecific hybrids have been reported, however, between plains cottonwood and named species to the north and west. In southern Alberta, Canada, plains cottonwood is reported to cross and introgress readily with balsam poplar *(Populus balsamifera* L.), narrowleaf cottonwood *(P. angustifolia* James), and possibly quaking aspen *(P. tremuloides* Michx.) *(4)*. Lanceleaf cottonwood *(P. × acuminata* Rydb.) is regarded as an interspecific hybrid between narrowleaf cottonwood *(P. angustifolia* James), which occurs from northern New Mexico, Nebraska, and North Dakota to southern Alberta, and plains cottonwood *(P. deltoides* var. *occidentalis) (14)*. Other reported interspecific hybrids involving plains cottonwood include *Populus × jackii* Sarg. *(P. balsamifera × deltoides* var. *occidentalis)*, and *Populus × polygonifolia* Bernard *(P. balsamifera × deltoides* var. *occidentalis* × tremuloides *(4)*.

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Populus grandidentata Michx. Bigtooth Aspen

Salicaceae Willow family

Paul R. Laidly

Bigtooth aspen *(Populus grandidentata)*, also called largetooth aspen, poplar, or popple, is a medium-sized deciduous hardwood tree of northeastern North America. It is short lived but grows rapidly, especially the first 30 years, on sandy upland soils and flood plains. Easily reproduced from seed or sucker shoots, it quickly reforests disturbed sites where it builds soil and protects seedlings of slower growing species. The soft, light-colored wood is used mostly for paper pulp. Wildlife use the foliage, twigs, and buds as food.

Habitat

Native Range

Bigtooth aspen (fig. 1) is native to northeastern and north-central United States and southeastern Canada. Its range extends from Cape Breton Island, Nova Scotia, west to southeastern Manitoba, south through Minnesota and Iowa to extreme northeastern Missouri, and east to southern Illinois, Kentucky, Virginia, and Delaware. It is also found locally in western North Carolina and northwestern Tennessee. In Canada, the greatest abundance of bigtooth aspen is in southwestern Quebec and southeastern Ontario *(4)*.

Climate

Bigtooth aspen spans a range of climatic conditions from the marine climate along the Atlantic coast to the continental climate of Minnesota and southwestern Ontario. Summers are humid and moisture is adequate at all seasons *(4,7)*.

Mean annual precipitation ranges from a low of 510 mm (20 in) on the prairie border in Manitoba to a high of 1520 mm (60 in) in the Maritime Provinces. North to south mean annual precipitation ranges from 510 to 1270 mm (20 to 50 in) with one-half or more occurring during the growing season. Mean annual snowfall exceeds 127 cm (50 in) where bigtooth aspen is most abundant and of best form. Mean annual snowfall exceeds 250 cm (100 in) in the Upper Peninsula of Michigan and the Northeast and reaches a maximum of 300 cm (120 in) in Nova Scotia *(7)*. Areas near Lake Superior in the Upper Peninsula of Michigan often receive more than 500 cm (200 in) of snowfall.

January temperatures average -18° C (0° F) in the North and 2° C (35° F) in the South. Temperatures of -46° C (- 50° F) have been recorded at the northern limit of bigtooth aspen.

Average July temperatures range from 16° C (60° F) in the North to 26° C (78° F) in the South. Temperatures higher than 38° C (100° F) have been recorded throughout its range.

Soils and Topography

Bigtooth aspen is capable of growing on a wide range of sites but is far less adaptable than quaking aspen *(Populus tremuloides)*. It is most abundant on sands, loamy sands, and light sandy loams, but it is found as a single tree or minor stand component on any soil, from rock outcrops to heavy clays. Bigtooth aspen develops best on moist, fertile sandy uplands where the depth to water table is no more than 1.5 m (5 ft), and site quality decreases rapidly as the depth to water table approaches 0.6 m (2 ft). Within this zone, a stagnant water table is much more detrimental than the lateral movement of water. Stands generally are unmerchantable if located on soils with an impermeable stratum at 0.3 m (1 ft) or less or a permeable subsoil that is dry to 1.5 m (5 ft) in the summer. Good soil aeration is essential for good growth of bigtooth aspen *(3,4,5,7)*. Soils on which bigtooth aspen most commonly grow are in the orders Spodosols, Alfisols, and Inceptisols.

Although bigtooth aspen can grow at sea level and has been found at altitudes over 915 m (3,000 ft) in North Carolina, it is most abundant and develops best on flat to gently rolling terrain of floodplains or lower slopes of the uplands between 150 to 610 m (500 to 2,000 ft) in altitude.

Associated Forest Cover

Bigtooth aspen is found in pure aspen forest covers either singly or in various combinations with quaking aspen and balsam poplar *(Populus balsamifera)*. Balsam poplar is a minor component of this combination on the dry-mesic sites and bigtooth aspen is a minor component on the wet-mesic sites *(4)*.

The species is a major component of the forest cover type Aspen (Society of American Foresters Type 16) and is a minor component in the following types *(8)*:

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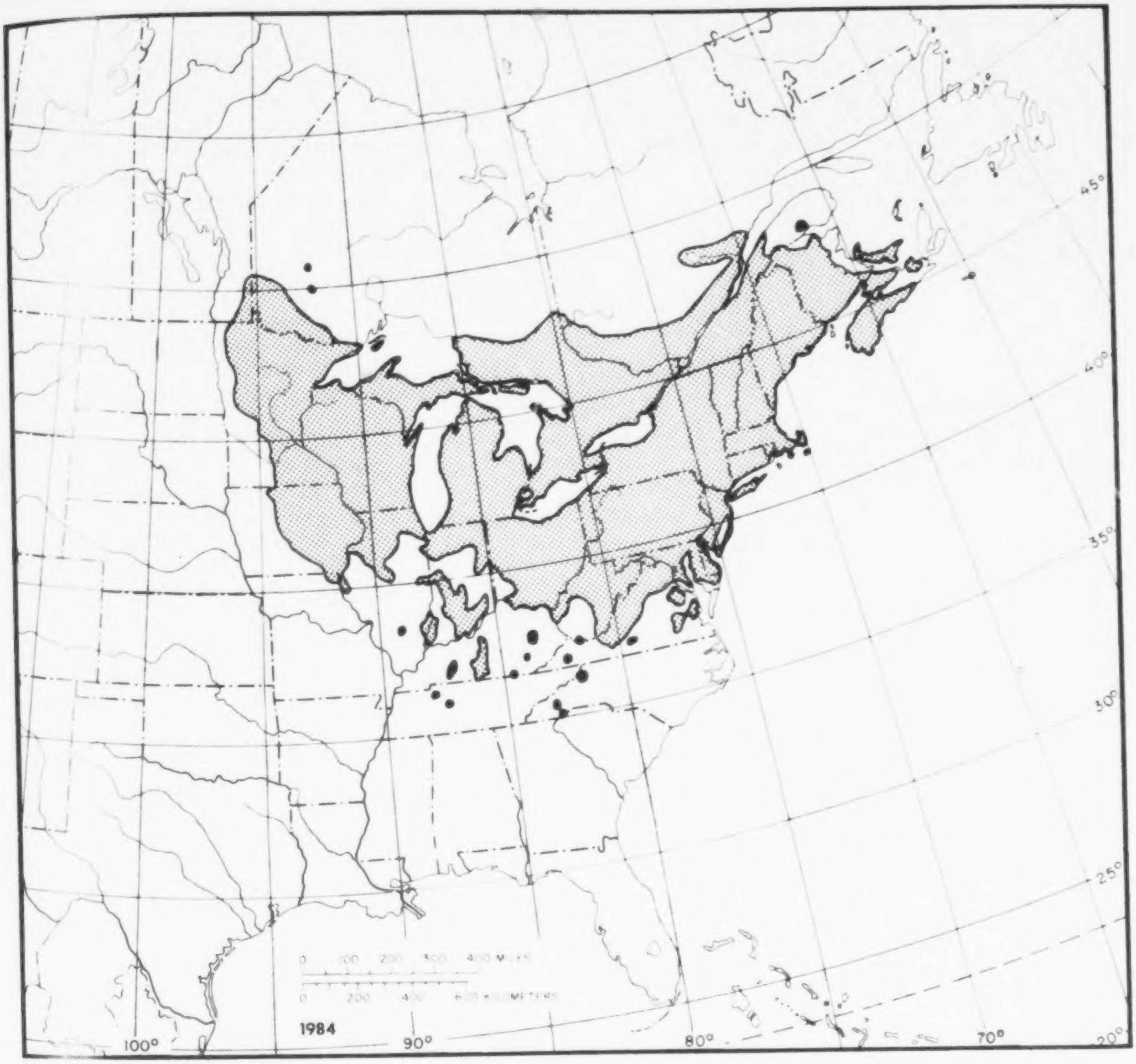
45°
40°
35°
30°
25°
20°
100°
90°
80°
70°
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
1984

Figure 1—*The native range of bigtooth aspen.*

1	Jack Pine
5	Balsam Fir
14	Northern Pin Oak
15	Red Pine
17	Pin Cherry
18	Paper Birch
19	Gray Birch–Red Maple
21	Eastern White Pine
25	Sugar Maple–Beech–Yellow Birch
32	Red Spruce
33	Red Spruce–Balsam Fir
35	Paper Birch–Red Spruce–Balsam Fir
37	Northern White-Cedar
43	Bear Oak
46	Eastern Redcedar
60	Beech–Sugar Maple
108	Red Maple

In the northern part of its range, common tree associates are quaking aspen, balsam poplar, balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), gray birch (*B. populifolia*), jack pine (*Pinus banksiana*), red pine (*P. resinosa*), red maple (*Acer rubrum*), and white spruce (*Picea glauca*). To the south and east, common tree associates are sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), bur oak (*Q. macrocarpa*), northern pin oak (*Q. ellipsoidalis*), white oak (*Q. alba*), eastern white pine (*Pinus strobus*), basswood (*Tilia americana*), pin cherry (*Prunus pensylvanica*), black cherry (*P. serotina*), and sassafras (*Sassafras albidum*).

Common shrub associates are chokeberry (*Prunus virginiana*), downy serviceberry (*Amelanchier arborea*), dogwood (*Cornus* spp.), willow (*Salix* spp.), beaked hazel (*Corylus cornuta*), speckled alder (*Alnus rugosa*), highbush cranberry (*Viburnum trilobum*), American hazel (*Corylus americana*), and sweetfern (*Comptonia peregrina*). Common ground flora are blueberry (*Vaccinium* spp.), teaberry (*Gaultheria procumbens*), bracken (*Pteridium aquilinum* var. *latiusculum*), fly honeysuckle (*Lonicera canadensis*), smooth sumac (*Rhus glabra*), dwarf bush-honeysuckle (*Diervilla lonicera*), and strawberry (*Fragaria* spp.) (*4,7,8*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Bigtooth aspen is normally dioecious; flowering begins at about age 10. Flowers are borne in drooping catkins, 5 to 7.5 cm (2 to 3 in) long, that are tan-colored at maturity. Bracts have 5 to 7 clefts and capsules are narrow and cone-shaped. Flowering precedes foliation and seed is dispersed before leaves are fully expanded. Female receptivity tends to begin before male pollen shed and lasts longer, but the mean dates of peak receptivity and pollen shed are closely allied. The timing of receptivity or pollen shed varies little intraclonally but varies significantly interclonally. The duration of active flowering is shorter for bigtooth aspen than for quaking aspen (*3,4,7,9*).

Air temperature seems to be the principal factor affecting the time and duration of flowering. In southern Ontario flowering occurs in late April; in southeastern lower Michigan flowering time is late April to early May; and in northern lower Michigan and northern Minnesota flowers appear in early to mid-May. Dehiscence of the capsule and seed dispersal take place about 4 weeks after flowering. Bigtooth aspen flowers, foliates, and disperses seeds about 10 days later than quaking aspen (*3,4,7*).

Seed Production and Dissemination—Seeds are pear-shaped, with a tuft of long silky hair attached to the narrow end. Good seed crops are produced every 2 or 3 years, but light seed crops are produced annually. Seeds are very light averaging approximately 5.6 million/kg (2.54 million/lb) with hair and are dispersed by wind for long distances from the parent tree (*4*). A single tree may produce more than 1.5 million seeds (*3*).

Seedling Development—Seedlings do not commonly occur in nature, in spite of extremely high production and high seed viability (more than 80 percent germination under laboratory conditions) (*3,4*). The uncommon occurrence has various causes: competition from other plants, short seed viability (2 or 3 weeks), the presence of a germination and growth inhibitor in the seed hairs, lack of moisture, high seedbed temperatures, susceptibility to fungal attack, and the chemical nature of some soils.

Germination is epigeal. Bare, moist soil is essential for seed germination and seedling establishment. If ground moisture is adequate, seeds usually germinate in 1 to 2 days. When the seed coat is ready to rupture, a typical time table for seedling development is as follows (*4*):

24 h	Radical emerges from seed and contacts soil; fine hairs develop at junction of radical and hypocotyl.
48 h	Hypocotyl elongates and raises cotyledons above ground.
144 h	Cotyledons expand and shed testa; radical penentrates soil about 10 mm (0.4 in).
1 yr	Seedling is 15 to 20 cm (6 to 8 in) tall; root spread is about 15 to 25 cm (6 to 10 in) deep and as much as 40 cm (16 in) wide.
2 yr	Seedling is 30 to 60 cm (12 to 24 in) tall.
3 yr	Seedling is 90 to 120 cm (36 to 48 in) tall.

Abundant moisture can greatly increase the first year's height growth, but competition from brush and weeds can easily eliminate 1-year-old seedlings.

Vegetative Reproduction—Suckering is the most common mode of reproduction. Suckers usually develop from shallow, cordlike lateral roots. These roots range from 0.5 to 11.4 cm (0.2 to 4.5 in) in diameter with the greatest proportion of suckers on roots less than 2.5 cm (1.0 in) in diameter. Sucker-bearing roots lie about 7.5 cm (3.0 in) deep in the mineral soil but can be as deep as 17.8 cm (7.0 in) (*4*). Sucker-bearing roots tend to be deeper for bigtooth aspen than for quaking aspen. Sprouts from stump and root collar are rare but develop more frequently in bigtooth than quaking aspen (*9*).

Sucker initiation is attributed to an increase in soil temperature and relief from the apical dominance effect *(3,4)*. Almost any disturbance—tree cutting, brush removal, fire, or ground scarification—can result in some degree of suckering *(2,3,5)*. Existing stands continually produce suckers but most of them are weak and die within a few years *(4,7)*.

Vegetative reproduction results in the formation of male and female clones that range from a few to several trees and occupy from 0.004 to 1.5 ha (0.01 to 3.8 acres) *(3,4)*.

Suckering ability varies significantly interclonally but no relation exists between size of clone and suckering ability. A single clone tends to exclude the invasion of other clones on a particular area, but the intermixing of "clone territories" to form a stand is common. In mixed stands of bigtooth aspen clones and quaking aspen clones, the clonal boundaries between the two species are well defined; the clonal boundaries within species are less distinct *(1,3,4,9)*.

After a stand is logged or killed by fire, suckering normally produces from 8,000 to 60,000 stems per hectare (3,200 to 24,000/acre). Age of parent stand, residual overstory, season of cutting, intensity of fire, and amount of ground scarification affect the abundance and vigor of suckers *(3,4,5,9)*. Suckers have been produced more than 30 m (100 ft) from the parent tree when invading open fields *(2)*, but 10 m (33 ft) is a more likely maximum within a stand *(6)*. Because of the existing root system, suckers grow faster than seedlings and often reach 0.9 to 1.8 m (3 to 6 ft) in height the first year.

Reproducing bigtooth aspen from stem cuttings is difficult. However, rootability can be improved if the cuttings have expanding foliar buds or are treated with indolebutyric acid *(4,7)*. Root cuttings have a good capacity to produce suckers. Interclonal variation in rootability of cutting is large.

Sapling and Pole Stages to Maturity

Growth and Yield—Normally, mature bigtooth aspen trees (fig. 2) are 18 to 24 m (60 to 80 ft) tall and 20 to 25 cm (8 to 10 in) in d.b.h. On the best sites, bigtooth aspen can attain a height of 30 m (100 ft) at 50 to 60 years of age *(3,4,5)*. Height growth is rapid for the first 30 years and slows markedly thereafter. Quaking aspen tends to have slower height growth initially but maintains this growth longer. Stand basal area seldom exceeds 34.4 m²/ha (150 ft²/acre).

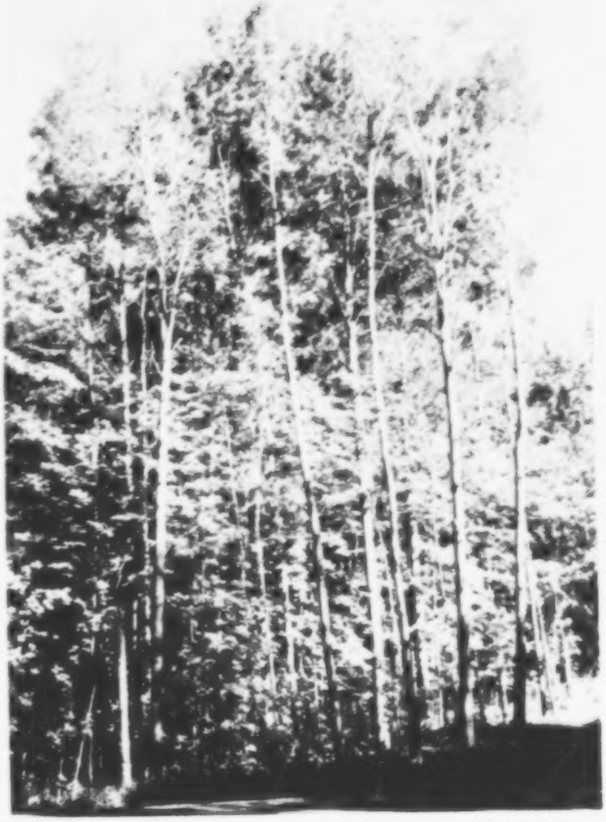

Figure 2—*A stand of bigtooth aspen on the Nicolet National Forest in Wisconsin.*

Empirical yields for 50-year-old bigtooth aspen in northern lower Michigan range from 100.8 m³/ha (1,440 ft³/acre) on site index 15 m (50 ft) sites to 296.8 m³/ha (4,240 ft³/acre) on site index 24 m (80 ft) sites (table 1) *(5)*. For bigtooth aspen, site index is determined at base age 50 years. Stands begin to deteriorate from rot fungi at 40 to 45 years of age on the poor sites and at 50 to 70 years of age on the better sites. Large single cull trees more than 100 years old are found. Bigtooth aspen appears to be more resistant to disease than quaking aspen.

Rooting Habit—Suckers remain connected to parent roots even after they develop their own root system. Adventitious roots develop at the basal part of the sucker or on the parent root near the sucker base. Cordlike root connections between the sucker and parent root remain alive until one of the two trees dies *(4)*.

Bigtooth aspen's root system is shallow and wide spreading. Strong, vertical, and penetrating roots near the base of the tree, and sinker roots developing

Table 1—Empirical yield table for bigtooth aspen in northern lower Michigan by age and site index[1]

Site index[2] and age (yr)	Mean height[3]	Mean d.b.h.	Basal area	Merchantable volume[4]
	m	*cm*	*m²/ha*	*m³/ha*
SI 15 m				
30	13.7	13	16.1	28.0
40	14.6	17	20.4	84.0
50	15.2	18	20.7	100.8
60	15.5	19	19.7	100.8
SI 18 m				
30	16.2	15	20.7	78.4
40	17.7	19	24.6	140.0
50	18.3	20	24.8	156.8
60	18.6	21	23.2	151.2
SI 21 m				
30	18.9	17	25.3	140.0
40	20.4	20	29.2	207.2
50	21.3	22	28.2	218.4
60	21.6	23	25.7	207.2
SI 24 m				
30	21.6	19	31.9	224.0
40	23.5	22	34.9	296.8
50	24.4	25	32.1	296.8
60	24.7	27	28.9	274.4
	ft	*in*	*ft²/acre*	*ft³/acre*
SI 50 ft				
30	45	5.1	70	400
40	48	6.6	89	1,200
50	50	7.1	90	1,440
60	51	7.3	86	1,440
SI 60 ft				
30	53	5.9	90	1,120
40	58	7.3	107	2,000
50	60	8.0	108	2,240
60	61	8.2	101	2,160
SI 70 ft				
30	62	6.6	110	2,000
40	67	8.0	127	2,960
50	70	8.8	123	3,120
60	71	9.2	112	2,960
SI 80 ft				
30	71	7.4	139	3,200
40	77	8.8	152	4,240
50	80	9.8	140	4,240
60	81	10.5	126	3,920

[1] All trees 1.5 cm (0.6 in) and larger in d.b.h.
[2] Height of dominants and codominants at 50 years.
[3] Dominants and codominants.
[4] Gross inside bark volume to a 10 cm (4.0 in) diameter inside bark.

from the lateral roots, provide good anchorage. Four to five well-developed lateral roots originate from the base of the tree and branch within 0.6 m (2 ft). The lateral spread of roots is usually 10 to 20 m (33 to 66 ft) under forested conditions. Bigtooth aspen's root system tends to be deeper, to be less branched, and to have fewer adventitious roots than quaking aspen's root system *(4,9)*.

Reaction to Competition—Bigtooth aspen is classed as very intolerant of shade. It cannot successfully reproduce under its own shade *(3,7)*, and seedlings must be kept free of competing brush and grasses. However, sucker growth is rapid enough to outgrow its competition. Leaving as little as 5.7 to 8.0 m²/ha (25 to 35 ft²/acre) basal area in the residual overstory can severely limit sucker initiation and growth. Severing all stems 5.0 cm (2.0 in) and larger is recommended for producing well-stocked vigorous sucker stands *(5)*.

Mortality is very high in young sucker stands, but this acts as a natural thinning agent. Trees begin to express dominance at 7 to 10 years, and potential crop trees can often be identified by age 10. Trees die throughout the life of the stand until 620 to 1,235 stems per hectare (250 to 500/acre) remain at the end of the rotation.

Bigtooth aspen responds well to thinning for producing small saw-log and veneer material. Only well-formed, disease-resistant clones on site index 21 m (70 ft) or better areas should be considered for producing sawtimber and veneer *(5)*.

Clearcutting is the best method for harvesting stands because the completeness of the overstory removal determines the establishment and vigor of the new stand. Rotation lengths are 30 to 40 years on the poorest sites, and 50 to 60 years on the best sites because stands deteriorate rapidly when held to greater ages. With proper harvesting and site preparation bigtooth aspen can continually occupy a site. Otherwise, it will be succeeded by the more shade-tolerant hardwood and coniferous species *(3)*.

Damaging Agents—Bigtooth aspen is subject to a number of agents that cause damage and mortality. Fire can easily kill these thin-barked trees or reduce their growth and provide entry points for disease organisms. Hailstorms may defoliate trees and severely scar stems and provide similar entry points. Heavy thinning may subject the residual stems to sunscalding. Windthrow is not a problem but wind breakage is common at cankered and borer-infested portions of the stem.

Hypoxylon canker *(Hypoxylon mammatum)* is the most serious disease of the aspens. Trees often are girdled or subjected to wind breakage, but bigtooth aspen is much more resistant to Hypoxylon canker than quaking aspen. Heart rot *(Phellinus tremulae)* can cause serious volume loss and stand deterioration when stands are held beyond rotation age.

Ganoderma applanatum and *Armillaria mellea* can cause extensive root decay. Shepherd's crook (*Venturia macularis*) may repeatedly kill new terminal growth in young stands (*2,4,7,9*). Clones vary greatly in resistance to disease attack and damage.

The forest tent caterpillar (*Malacosoma disstria*) and the large aspen tortrix (*Choristoneura conflictana*) have periodically defoliated extensive areas of aspen. Populations of these insects usually persist for 2 or 3 years and then suddenly collapse. Growth loss can be substantial but few trees are killed (*2,4,7,9*).

The poplar borer (*Saperda calcarata*) is the most serious wood borer in aspen. Extensive boring degrades large trees and subjects stems to wind breakage. Wood borers of several species can provide infection points for Hypoxylon canker and other fungi. In turn, defoliating insects may cause an increase in populations of wood borers (*2,4,7,9*).

When their populations are high, deer and hare can heavily browse young stands. This is seldom a problem in dense stands, however, because browsing helps thin these stands. Beaver can kill large portions of stands both by flooding and by cutting trees (*2,5,9*).

Special Uses

Typical management of aspen stands does not distinguish between bigtooth aspen and quaking aspen, and their uses are not differentiated. The aspen forests contribute significantly to maintaining other resources. It is no accident that the native range of ruffed grouse coincides with the native range of the aspens. Aspen leaves and staminate flower buds provide ruffed grouse with their most important yearlong food resource. Aspen suckers are a favored winter food of moose and are heavily browsed by white-tailed deer. Although aspen is not the most palatable browse, an abundance and wide distribution of small clearcuttings are essential for maintaining a good deer population. The bark, leaves, twigs, and branches of aspen are preferred by beaver (*2,9*).

Because aspen is deciduous, more snow accumulates on the ground in aspen than in coniferous stands. Thus, soils are better insulated from freezing and snowmelt enters the soil rather than running overland. Because of aspen's ability to produce abundant suckers, fire-killed stands are rapidly revegetated. Similarly, aspen can be harvested on slopes without seriously affecting erosion or water quality. Aspen often is perpetuated on areas where soil stabilization poses a problem (*2*).

Aspen bark has been pelletized for supplemental cattle feed and fuel. Although the vast quantity of these pellets comes from quaking aspens bark, no distinction has been made between bigtooth aspen and quaking aspen in the pelletizing process.

Genetics

Population Differences

Recognizing the inter- and intraspecific clonal variation in aspen stands can lead to definite upgrading of the quality of aspen in growth, form, and disease resistance. In mixed stands of bigtooth aspen and quaking aspen on dry exposed sites, bigtooth aspen clones have superior growth and disease resistance (*5,6*). The interclonal variation in rootability should be recognized when stands are established from stem and root cuttings.

Hybrids

Natural hybrids of bigtooth aspen and quaking aspen do occur, but less frequently than might be expected, because of differences in time of flowering. When hybridization occurs, it is most likely to be between male quaking aspen and female bigtooth aspen (*3,4,9*).

The best known interspecific hybrid is *Populus alba* × *P. grandidentata* (*P.* × *rouleauiana* Boivin). Growth is superior to native bigtooth aspen on dry, sandy soils, but its development is maximized on fertile, moist loamy soils. Seed production and suckering are generally low and branchiness and form are poor. *P.* × *canescens* × *P. grandidentata* has shown good growth but poor rootability. *P.* × *canescens* × *P. alba* × *P. grandidentata* has shown both good growth and good rootability. Additional crosses with bigtooth aspen have been made but are generally of lower quality.

Intraspecific crosses of bigtooth aspen have been difficult to establish in plantings and have slow early growth. Bigtooth aspen has 19 pairs of chromosomes ($2n=38$).

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Populus heterophylla L. Swamp Cottonwood

Salicaceae **Willow family**

R. L. Johnson

Swamp cottonwood (*Populus heterophylla*) is of secondary importance among bottom-land hardwoods. The species, sometimes referred to as black cottonwood, river cottonwood, downy poplar, or swamp poplar, may grow on sites that are too wet for other native poplars. It is a difficult species to grow from cuttings, a characteristic that limits its commercial value.

Habitat

Native Range

Swamp cottonwood (fig. 1) inhabits the wet bottom lands and sloughs of the Coastal Plain from Connecticut and southeastern New York to Georgia and

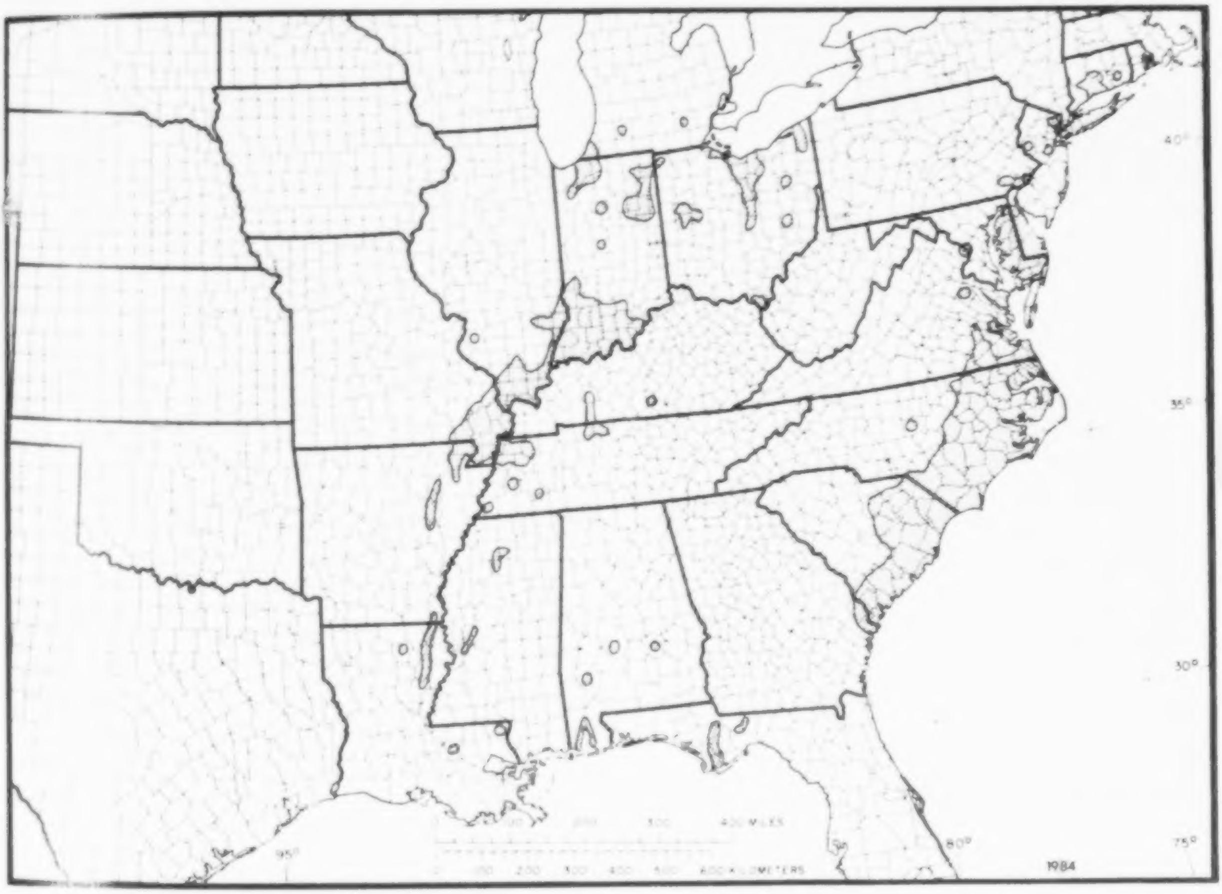

Figure 1—*The native range of swamp cottonwood.*

The author is Principal Silviculturist, Southern Forest Experiment Station, New Orleans, LA northwestern Florida, west to Louisiana. It grows north in the Mississippi Valley to southeastern Missouri, western Tennessee, Kentucky, southern Illinois, Indiana, Ohio, and southern Michigan *(5)*.

Climate

The climate is humid throughout the range of swamp cottonwood. Average annual rainfall varies from about 890 mm (35 in) in northern Indiana to 1500 mm (59 in) in southern Louisiana. Approximately 1140 to 1240 mm (45 to 49 in) of rain falls annually along the Atlantic coast, nearly half of it from April through August. Yearly temperatures average 10° to 13° C (50° to 55° F) in the North to 18° C (65° F) along the south Atlantic coast and 21° C (70° F) on the gulf coast. Minimum annual temperatures range from -29° C (- 20° F) in the North to -1° C (30° F) in the South. Frost-free days range from 180 to 300.

Soils and Topography

Though most often found on heavy clays, swamp cottonwood also grows on the edges of, but not in, the muck swamps of the Southeast. Optimum growth and development is in the deep, moist soils of shallow swamps and low-lying areas near tidewater *(4)*.

Sites that are too wet for eastern cottonwood *(Populus deltoides)* will support swamp cottonwood. Examples are shallow swamps, sloughs, and very wet river bottoms where the water table remains near the soil surface for all but 2 or 3 months in the summer and early fall. In the southern part of its range, low, wet flats provide the driest sites occupied by swamp cottonwood. However, in southern Illinois it is a dominant or codominant tree on soils with available moisture varying from 3 to 21 percent for the 61- to 76-cm (24- to 30-in) layer *(4)*.

Swamp cottonwood grows naturally on at least eight major soil types common to the Midsouth: Alligator, Amagon, Arkabutla, Forestdale, Perry, Rosebloom, Sharkey, and Tensas. The soils represent several families and the orders Alfisols, Inceptisols, and Entisols. They range from 4.6 to 5.9 in pH and from 24 to 65 percent clay in the surface 0.3 m (1 ft) *(1)*.

Associated Forest Cover

Swamp cottonwood is sparse throughout its range and is not a major species in any forest cover type. It is most often found in the following types *(2)*: Baldcypress (Society of American Foresters Type 101), Baldcypress–Tupelo (Type 102), and Water Tupelo–Swamp Tupelo (Type 103).

Common tree associates include sandbar willow *(Salix exigua)*, black willow *(S. nigra)*, peachleaf willow *(S. amygdaloides)*, green ash *(Fraxinus pennsylvanica)*, water hickory *(Carya aquatica)*, sycamore *(Platanus occidentalis)*, sugarberry *(Celtis laevigata)*, red maple *(Acer rubrum)*, American elm *(Ulmus americana)*, pumpkin ash *(F. profunda)*, Carolina ash *(F. caroliniana)*, waterlocust *(Gleditsia aquatica)*, persimmon *(Diospyros virginiana)*, and overcup oak *(Quercus lyrata)*.

Major small tree and shrub associates are waterelm *(Planera aquatica)*, buttonbush *(Cephalanthus occidentalis)*, swamp-privet *(Forestiera acuminata)*, and possumhaw *(Ilex decidua)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Swamp cottonwood is dioecious. Flowers are proteranthous, appearing from March to May. Staminate catkins are rather stiffly pendant, oblong, cylindric, and 5 to 10 cm (2 to 4 in) long; pistillate catkins are 5 to 15 cm (2 to 6 in) long, pendulous, slender, and raceme-like. Pollination is by wind. Fruits ripen and the seeds fall from April through July.

Seed Production and Dissemination—Trees start seed production at about 10 years. Reddish-brown obovoid seeds number about 330,700/kg (150,000/lb) *(9)*. Seeds are very small, light in weight, and tufted with hairs, features that allow them to be blown over 100 m (330 ft) by wind and to float for a considerable distance in water. Water is an important transporting agent since the bottom lands normally flood during the seedfall period. Numerous seeds are produced annually, but under natural field conditions they remain viable for no more than a week or two.

Seedling Development—Germination is epigeal. Best seedling establishment is from seeds that quickly settle on unshaded, moist mineral soil in shallow swamps, deep sloughs, and along often-flooded creeks or rivers. Seedlings require nearly full sunlight to survive and grow. They also need an abundance of moisture, especially during the early part of the growing season. Seedlings usually occur in groups but seldom cover a large area *(4)*. Early growth is relatively rapid but will not match that of eastern cottonwood. On a well-drained soil in southern Illinois, swamp cottonwood seedlings grew at about the same rate as silver maple seedlings.

Vegetative Reproduction—Cuttings from juvenile plants will root but probably not as well as those of eastern cottonwood *(4)*. Stumps less than 30 cm (12 in) in diameter are likely to produce sprouts.

Sapling and Pole Stages to Maturity

Growth and Yield—The largest swamp cottonwood trees on record are 35 to 40 m (115 to 130 ft) tall and 165 to 190 cm (65 to 75 in) in d.b.h. *(3,8)*. Trees are considered mature at about 30 m (100 ft) tall and 75 to 90 cm (30 to 36 in) d.b.h. Annual height growth on poorly drained sites is slightly faster over a 30-year period than that of green ash, about 0.8 m (2.5 ft). Diameter growth on a good site in the South may approach 20 cm (8 in) in 10 years *(4)*. Swamp cottonwood grows little after 40 or 50 years and seldom remains sound after 80 years *(4)*. Large trees often are crooked and short boled. Trees with three merchantable logs are exceptional.

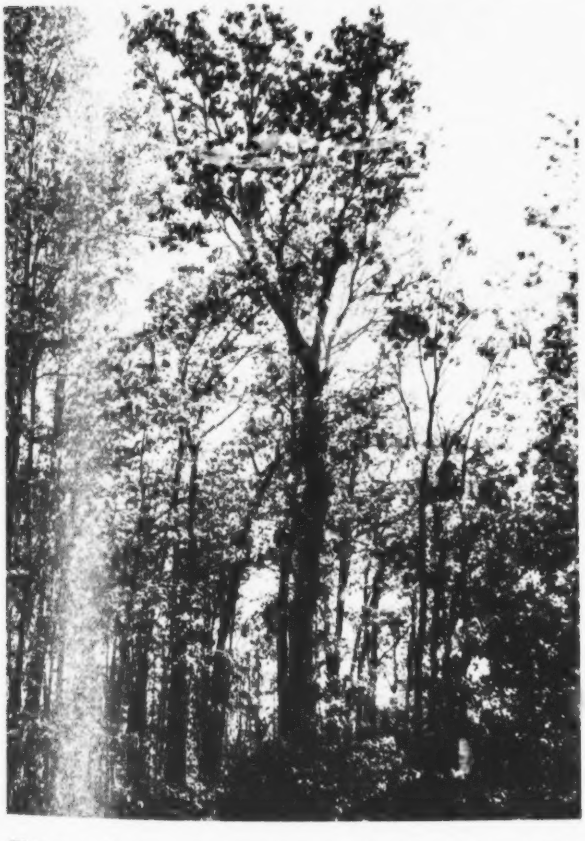

Figure 2—Swamp cottonwood tree on bottom-land site in Leflore County, MS.

Per-hectare volumes are unknown for this species since it is nearly always a single tree or grows in very small patches (fig. 2). Based on known volumes for eastern cottonwood *(6)*, a pure stand of mature swamp cottonwood would likely yield 280.0 to 350.0 m^3/ha (20,000 to 25,000 fbm/acre, Doyle log rule).

Rooting Habit—The root system of swamp cottonwood is probably shallow like that of eastern cottonwood and most other lowland species. Poplars in general have strong horizontal surface roots from which vertical plunging roots develop. Length of horizontal roots can be considerable. Plunging roots are limited in development by the water table or soil condition.

Reaction to Competition—Swamp cottonwood is classed as intolerant of shade, though probably less so than eastern cottonwood. Individuals may survive partial shade when they are young, but older trees require full sunlight.

Damaging Agents—There are no reported insect or disease problems associated specifically with swamp cottonwood. But the ones that attack eastern cottonwood probably also damage swamp cottonwood. Important insect enemies include the cottonwood leaf beetle *(Chrysomela scripta)*, cottonwood twig borer *(Gypsonoma haimbachiana)*, poplar borer *(Saperda calcarata)*, and the cottonwood borer *(Plectrodera scalator)*. Among the more important diseases are Melampsora leaf rust *(Melampsora medusae)* and a number of canker diseases, including *Septoria*, *Cytospora*, and *Fusarium (7)*.

Special Uses

There is no market specifically for the small volume of swamp cottonwood harvested. The wood resembles that of eastern cottonwood and is generally sold as such. Among the uses for cottonwood lumber and veneer are boxes, crates, and interior parts for furniture. Pulpwood is used in high-grade book and magazine paper.

To date, few other uses have been found for the species. It is rarely cultivated for ornament, does not produce important wildlife food, and is important to flood or erosion control only in very small, localized areas. Instead of swamp cottonwood, a closely related species, eastern cottonwood, is chosen for planting because it outperforms swamp cottonwood on all except the wettest sites.

Genetics

The species is rare in tree collections and has received little attention from geneticists. There are no reported races or hybrids.

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Populus tremuloides Michx. Quaking Aspen

Salicaceae **Willow family**

D. A. Perala

Quaking aspen *(Populus tremuloides)* is the most widely distributed tree in North America. It is known by many names: trembling aspen, golden aspen, mountain aspen, popple, poplar, trembling poplar, and in Spanish, álamo blanco, and álamo temblón *(49)*. It grows on many soil types, especially sandy and gravelly slopes, and it is quick to pioneer disturbed sites where there is bare soil. This fast-growing tree is short lived and pure stands are gradually replaced by slower-growing species. The light, soft wood has very little shrinkage and high grades of aspen are used for lumber and wooden matches. Most aspen wood goes into pulp and flake-board, however. Many kinds of wildlife also benefit from this tree.

Habitat

Native Range

Quaking aspen (fig. 1) grows singly and in multistemmed clones over 111° of longitude and 48° of latitude for the widest distribution of any native tree species in North America *(48)*. The range extends from Newfoundland and Labrador west across Canada along the northern limit of trees to northwestern Alaska, and southeast through Yukon and British Columbia. Throughout the Western United States it is mostly in the mountains from Washington to California, southern Arizona, Trans-Pecos Texas, and northern Nebraska. From Iowa and eastern Missouri it ranges east to West Virginia, western Virginia, Pennsylvania, and New Jersey. Quaking aspen is also found in the mountains of Mexico, as far south as Guanajuato. Worldwide, only *Populus tremula*, European aspen, and *Pinus sylvestris*, Scotch pine, have wider natural ranges.

Climate

Climatic conditions vary greatly over the range of the species, especially winter minimum temperatures and annual precipitation. The known widest range of temperatures aspen has endured in the conterminous United States is in Montana, where January lows of -57° C (-70° F) and summer highs of 41° C (105° F) have been recorded. In Alaska and northwest Canada, part of the range lies within the permafrost zone, but quaking aspen grows only on the warmest sites free of permafrost *(28,91)*.

At the eastern end of the range, in the Maritime Provinces of Canada, the climate is mild, humid, and snowfall is extremely heavy, 300 cm (120 in) or more per year. Some representative climates for the northern and eastern limits of quaking aspen as well as for the warmer parts of its eastern range are as follows *(78)*:

	Interior Alaska	*Gander, NF*	*Ft. Wayne, IN*
Temperature, C:			
Minimum	-61	-34	-31
January average	-30	-7	-3
Maximum	38	32	41
July average	16	16	23
Precipitation, mm:			
Total	180	1020	860
Growing season	80	250	330
Frost-free days	81	160	176
Temperature, F			
Minimum	-78	-29	-24
January average	-22	19	27
Maximum	100	90	106
July average	61	61	73
Precipitation, in:			
Total	7	40	34
Growing season	3	10	13
Frost-free days	81	160	176

In the central Rocky Mountains, where altitude plays an important role in the distribution of aspen, the lower limit of its occurrence coincides roughly with a mean annual temperature of 7° C (45° F). In Colorado and southern Wyoming, quaking aspen grows in a narrow elevational belt of 2100 to 3350 m (6,900 to 11,000 ft). Average annual precipitation in this belt ranges from 410 to 1020 mm (16 to 40 in). The southern limit of the range of aspen in the Eastern United States is roughly delineated by the 24° C (75° F) mean July temperature isotherm. In Canada the mean annual degree-day sum of 700° C (1260° F) with a threshold temperature 5.6° C (42° F) coincides closely with the northern limit of the species *(51,69, 70,78,80)*.

Quaking aspen occurs where annual precipitation exceeds evapotranspiration. It is abundant in interior Alaska where annual precipitation is only about 180 mm (7 in) because evapotranspiration is limited by cool summer temperatures. In the interior west the 2.5 cm (1 in) average annual surface water runoff

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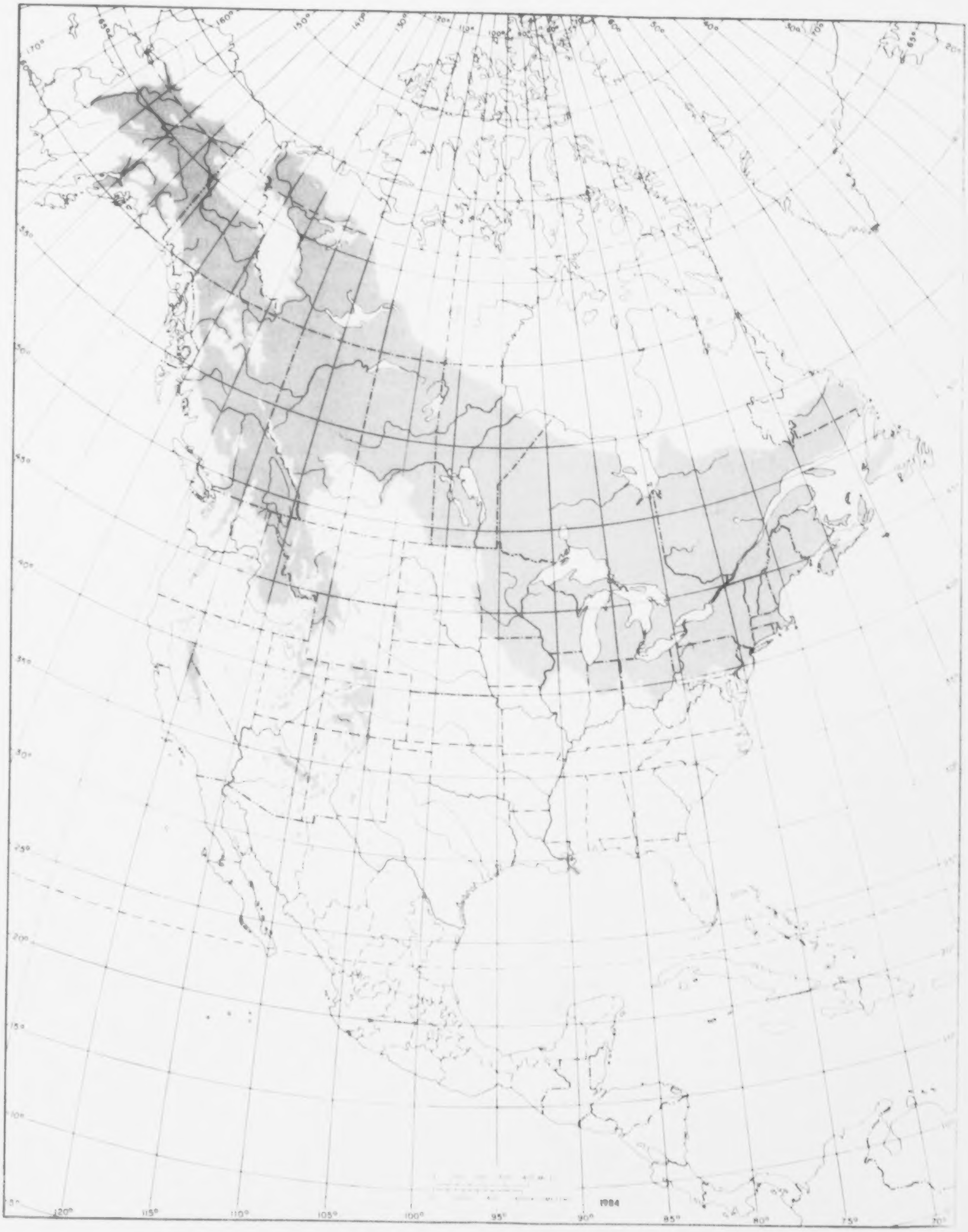
120°
115°
110°
105°
100°
95°
90°
85°
80°
75°
70°
1984

Figure 1—*The native range of quaking aspen.*

isopleth is more coincident with the range of aspen than is any isotherm. This isopleth also is coincident with the southern limit of aspen in the prairie provinces of Canada eastward to northwestern Minnesota and south to Iowa where high summer temperatures limit growth and longevity. In summary, the range of quaking aspen is limited first to areas of water surplus and then to minimum or maximum growing season temperatures *(33,71,91)*.

Soils and Topography

Quaking aspen grows on a great variety of soils (mainly Alfisols, Spodosols, and Inceptisols) ranging from shallow and rocky to deep loamy sands and heavy clays *(83)*. Only occasional scattered trees that seldom attain economic size occur on the coarser sands of glacial outwash, the shallowest soils of rock outcrops, and on some Histosols. In the West, it has become established on volcanic cinder cones, and in New England it is one of several species that colonizes immediately after landslides. In the Lake States, it often reforests mining waste dumps and abandoned borrow pits *(78)*.

Growth and development are strongly influenced by both physical and chemical properties of soil. The best quaking aspen stands in the Rocky Mountains and Great Basin are on soils developed from basic igneous rock, such as basalt, and from neutral or calcareous shales and limestones; the poorest are found on soils derived from granite. Some of the best stands of quaking aspen are in the northern part of the Lake States and in Manitoba and Saskatchewan, on Boralfs that have developed from the Keewatin drift, a gray glacial drift rich in lime. Good aspen soils are usually well drained, loamy, and high in organic matter, calcium, magnesium, potassium, and nitrogen. Because of its rapid growth and high nutrient demand, quaking aspen has an important role in nutrient cycling *(2,3,18,28,78)*.

Growth on sandy soils is often poor because of low levels of moisture and nutrients. On droughty sands in the western Great Lakes region, the site index at age 50 is usually less than 17 m (56 ft). On the better sandy loams it may be about 21 m (69 ft), and on silt loams 23 to 25 m (75 to 82 ft). The best aspen sites have been found on soils with silt-plus-clay content of 80 percent or more. Wood of the highest mean specific gravity (about 0.40) is produced on well-drained fine-textured soils, and that of the lowest mean specific gravity (about 0.35) on poorly drained soils *(28,71,78)*.

Internal drainage is critical. Water tables shallower than 0.6 m (2 ft) or deeper than 2.5 m (8.2 ft) limit aspen growth. Heavy clay soils do not promote the best growth because of limited available water and poor aeration *(35,57,78)*.

Aspen spans an elevational range from sea level on both Atlantic (Maine) and Pacific (Washington) coasts to 3505 m (11,500 ft) in northern Colorado. Near its northern limit, quaking aspen is found at elevations only up to 910 m (3,000 ft). In Baja, California, it does not occur below about 2440 m (8,000 ft). In Arizona and New Mexico it is most abundant between 1980 and 3050 m (6,500 and 10,000 ft); in Colorado and Utah, about 300 m (1,000 ft) higher. At either of its altitudinal limits the tree is poorly developed. In very high exposed places it becomes stunted, with the stem bent or almost prostrate from snow and wind; at its lower limit it is a scrubby tree growing along creeks *(28,70,78,91)*.

Quaking aspen is most abundant and grows best on warm south and southwest aspects in Alaska and western Canada. It is common on all aspects in the western mountains of the United States and grows well wherever soil moisture is not limiting. However, the best stands in the Southwest are more frequently found on the northerly slopes where more favorable moisture conditions prevail. Development is poor on physiographic positions with excessive droughtiness. In the prairie provinces of Canada, particularly near the border between prairie and woodland, the species is confined to the cooler and moister north and east slopes and to the depressions *(28,69,70,78)*.

Associated Forest Cover

Quaking aspen (fig. 2) grows with a large number of trees and shrubs over its extensive range. It is a major component of three forest cover types *(72)*, Aspen (Eastern Forest) (Society of American Foresters Type 16), Aspen (Western Forest) (Type 217), and White Spruce–Aspen (Type 251). It is a minor component of 35 other types and an occasional to rare component in 3 types.

Shrub species commonly associated with quaking aspen in the eastern part of its range include beaked hazel *(Corylus cornuta)*, American hazel *(C. americana)*, mountain maple *(Acer spicatum)*, speckled alder *(Alnus rugosa)*, American green alder *(A. crispa)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, raspberries and blackberries *(Rubus* spp.), and various species of gooseberry *(Ribes)* and willow *(Salix)*. Additional species occurring with quaking aspen in the prairie provinces include: snowberry *(Symphoricarpos* spp.), highbush cranberry *(Viburnum edule)*, limber honeysuckle *(Lonicera dioica)*, red-osier dogwood *(Cornus stolonifera)*, western serviceberry *(Amelanchier alnifolia)*, chokecherry *(Prunus virginiana)*, Bebb willow *(Salix bebbiana)*, and several species of rose *(Rosa)*. The latter two also occur in Alaska plus such additional species as Scouler willow *(Salix scouleriana)*, bearberry *(Arctostaphylos uva-ursi)*, russet buffaloberry *(Shepherdia canadensis)*, mountain cranberry *(Vaccinium vitis-idaea)*, and highbush cranberry. In the Rocky Mountains, shrubs commonly occurring with quaking aspen include mountain snowberry *(Symphoricarpos oreophilus)*, western serviceberry, chokecherry, common juniper *(Juniperus communis)*, creeping hollygrape *(Berberis repens)*, woods rose *(Rosa woodsii)*, myrtle pachistima *(Pachistima myrsinites)*, redberry elder *(Sambucus pubens)*, and a number of *Ribes* *(69,70,72,78,85,91)*.

Herbs characteristic of quaking aspen stands in the east include largeleaf aster *(Aster macrophyllus)*, wild sarsaparilla *(Aralia nudicaulis)*, Canada beadruby *(Maianthemum canadense)*, bunchberry *(Cornus canadensis)*, yellow beadlily *(Clintonia borealis)*, roughleaf ricegrass *(Oryzopsis asperifolia)*, sweetscented bedstraw *(Galium triflorum)*, sweetfern *(Comptonia perigrina)*, lady fern *(Athyrium filix-femina)*, bracken *(Pteridium aquilinum)*, and several species of sedges *(Carex* spp.) and goldenrods *(Solidago* spp.). In the West, the herbaceous component is too rich and diverse to describe. Forbs dominate most sites, and grasses and sedges dominate others *(72)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Quaking aspen is primarily dioecious. The pendulous flower catkins, 3.8 to 6.4 cm (1.5 to 2.5 in) long, generally appear in April or May (mid-March to April in New England, May to June in central Rockies) before the leaves expand *(28,66,78,91)*. Local clonal variation provides early and late flowering clones of each sex in most stands. In addition, certain flowers bloom later than others, usually those on the distal end of a given catkin or small catkins on spurlike shoots *(13)*. Maximum air temperatures above 12° C (54° F) for a period of about 6 days appear to be the principal factor governing timing of flowering. Flowers are pollinated by wind. The fruiting catkins are about 10 cm (4 in) long when mature, usually in May or June—about 4 to 6 weeks after flowering. Each catkin may bear several dozen one-celled capsules, light green, each nearly 6 mm (0.25 in) long. Each capsule contains about 10 small brown seeds, each of which is surrounded by tufts of long, white silky hairs. Although the flowers are typically unisexual, 10 to 20 percent of the predominantly female trees and 4 to 5 percent of the predominantly male trees bear perfect flowers. Trees in a given clone, therefore, are usually either all male or all female. Some studies in the eastern United States found male-to-female ratios of about 3 to 1 in natural populations; others have reported no deviation from an expected 1-to-1 ratio *(66,78)*. In the Colorado Rockies, male clones were more common at high elevations and female clones were more common at low elevations. Furthermore, female clones had faster radial growth than male clones, especially at lower elevations. This runs counter to the theory that the high metabolic cost of sexual reproduction for females is compensated for by reduced vegetative growth *(36)*.

Seed Production and Dissemination—Good seed crops are produced every 4 or 5 years, with light crops in most intervening years. Some open-grown clones may produce seeds annually, beginning at age 2 or 3. The minimum age for large seed crops is 10 to 20; the optimum is 50 to 70. One 23-year-old quaking aspen produced an estimated 1.6 million seeds *(51,59,78)*. Seeds are very light, 5,500 to 8,000 clean seeds per gram (156,000 to 250,000/oz).

Seeds begin to be dispersed within a few days after they ripen and seed dispersal may last from 3 to 5 weeks. The seeds, buoyed by the long silky hairs, can be carried for many kilometers by air currents. Water also serves as a dispersal agent *(78,91)*.

The viability of fresh fertile seeds is high (usually greater than 95 percent) but normally of short dura-

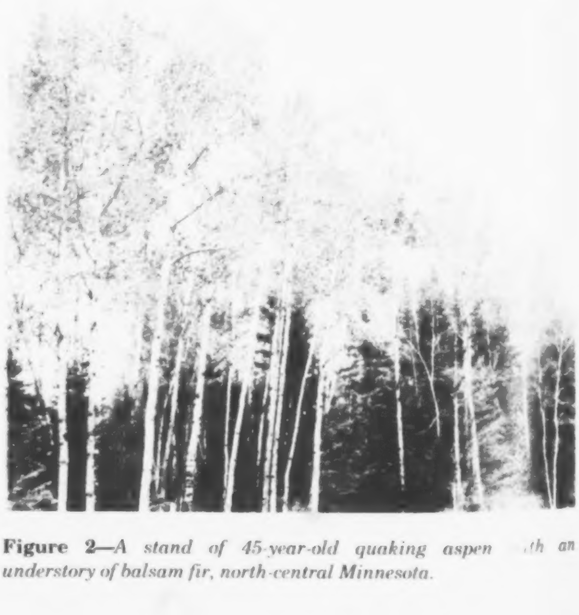

Figure 2—*A stand of 45-year-old quaking aspen with an understory of balsam fir, north-central Minnesota.*

tion. Under favorable conditions viability lasts only 2 to 4 weeks after maturity and may be much less under unfavorable conditions. When air dried and stored in polyethylene bags at –10° C (14° F), seed retains high viability for at least 1 year. Seedlings are sturdiest when germinated at 5° to 29° C (41° to 84° F) and grown at about 20° C (68° F). Ripe quaking aspen seeds are not dormant, and germination occurs within a day or two after dispersal if a suitably moist seedbed is reached. Because germintion declines rapidly after water potential exceeds -4 bars (-.4 MPa), a water-saturated seedbed is critical. Seeds germinate even when totally submerged in water or in the absence of light *(32,47,50,66,78,92)*.

Seedling Development—Germination is epigeal. The primary root of a seedling grows very slowly for several days, and during this critical period the young plant depends upon a brush of long delicate hairs to perform the absorptive functions and anchor the seedling to the seedbed. Exposed mineral soils are the best seedbeds and litter the poorest seedbeds *(28,51,60,78)*.

During the first year seedlings may attain a height of 15 to 30 cm (6 to 12 in) and develop a 20- to 25-cm (8- to 10-in) long taproot and from 30- to 40-cm (12- to 16-in) long laterals. During the second and third years, wide-spreading lateral roots are developed, reaching lengths of 2 m (6 ft) or more in the second year. Quaking aspen roots form ectomycorrhizae if suitable inoculum is present *(28,78,86)*.

Despite the abundance of aspen seed and high germinative capacity, few aspen seedlings survive in nature because of the short period of seed viability, unfavorable moisture during seed dispersal, high soil surface temperatures, fungi, adverse diurnal temperature fluctuations during initial seedling growth, and the unfavorable chemical balance of some seedbeds *(51,52)*.

Height growth of the young trees is rapid for about the first 20 years and slows thereafter. During the first several years, natural seedlings grow faster than planted seedlings but not as fast as suckers. High mortality characterizes young quaking aspen stands regardless of origin. In both seedling and sucker stands natural thinning is rapid, and trees that fall below the canopy stop growing and die within a few years *(78,93)*.

Vegetative Reproduction—The aggregation of stems (ramets) produced asexually from a single sexually produced individual (the genet) is termed a clone. In aspen a clone is formed from the root system of the seedling genet following an event (cutting, fire) that destroys the genet *(9)*.

Quaking aspen seedlings at 1 year of age are already capable of reproducing by root sprouts (suckers), and mature stands reproduce vigorously by this means *(19,43)*. Root collar sprouts and stump sprouts are produced only occasionally by mature trees but saplings commonly produce them *(77)*. Aspen clones vary widely in many characteristics, even over a small area. Members of a clone are indistinguishable but can be distinguished from those of a neighboring clone by electrophoresis and often by a variety of traits such as leaf shape and size, bark character, branching habit, resistance to disease and air pollution, sex, time of flushing, and autumn leaf color *(9,10,11,17,22,23,57,87)*. Clones typically have many ramets over an area up to a few tenths of a hectare in stands east of the Rocky Mountains *(45,76)*. In the Rockies, clones tend to be much larger—one Utah clone covered 43.3 ha (107 acres) and contained an estimated 47,000 ramets. Clone size in an aspen stand is primarily a function of clone age, number of seedlings initially established, and the frequency and degree of disturbance since seedling establishment *(46)*.

The root suckers (fig. 3) are produced from meristems on the shallow, cordlike lateral roots within 2 to 10 cm (1 to 4 in) of the soil surface *(28,81)*. In response to clone disturbance, the meristems may develop into buds and then elongate into shoots. Frequently, however, they remain in the primordial stage until stimulated to develop further. These preexisting primordia are visible as small bumps when cork is peeled off an aspen root *(63)*.

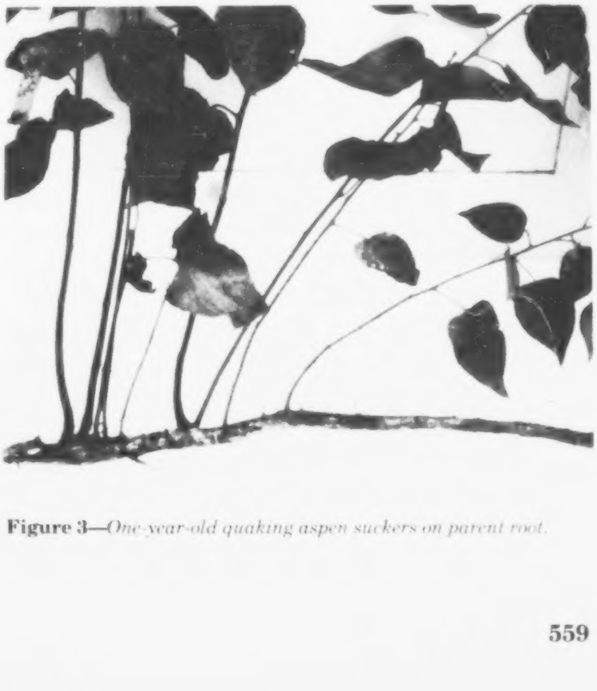

Figure 3—*One-year-old quaking aspen suckers on parent root.*

The development of suckers on aspen roots is suppressed by apical dominance exerted by auxin transported from growing shoots, while cytokinins, hormones synthesized in root tips, apparently initiate adventitious shoot development. When an aspen is cut, cytokinins accumulate in the roots, the supply of inhibitory auxins is eliminated, and suckers are initiated. If aspen is girdled, the downward transport of auxin again is stopped, but upward translocation of cytokinins via the xylem is unimpeded. Cytokinins in this case do not accumulate in the roots, with consequently less sucker production. Thus high cytokinin-to-auxin ratios favor shoot initiation while low ratios inhibit it. A gibberellic-acid-like growth regulator also stimulates shoot elongation after sucker initiation.

Carbohydrate reserves supply the energy needed by elongating suckers until they emerge at the soil surface to carry on their own photosynthesis. Therefore, the density of regeneration varies according to the level of these reserves. However, the number of suckers initiated by aspen roots is independent of variation in carbohydrate levels. Apical dominance by elongating suckers further limits the total amount of regeneration. Carbohydrates can be exhausted by grazing, repeated cropping or killing of sucker stands, or insect defoliation *(63,77,82)*.

Soil temperature is the most critical environmental factor affecting suckering. Initiation and development of suckers is optimum at about 23° C (74° F). High temperatures tend to degrade auxin and promote cytokinin production, which may account in part for the aspen invasion of grassland without apparent clone disturbance *(51,82)*.

Excess soil moisture (impeded aeration) or severe drought inhibit sucker production *(25,57,82)*.

Light is not needed for sucker initiation but is essential for secondary growth *(78)*. Large clonal differences in ability to produce suckers may be due to differences in growth regulators, carbohydrate reserves, and developmental stages of shoot primordia *(63)*. Some clones in the interior West are uneven-aged, suggesting weak apical control or high concentration of growth-promoting hormones so that they sucker at the least disturbance *(69,82)*.

Suckers are initially sustained by the root system of the parent tree, but they may form as much as 4.7 m (15.5 ft) of new main roots in 10 weeks. In contrast, suckers of some Utah clones produce only weak adventitious roots and depend on the distal parent root for sustenance. The parent root usually thickens at the point of sucker origin distal to the parent tree. This indicates that translocation of food produced by the sucker is toward the growing tip of the parent root, which usually becomes part of the new root system *(28,51,78,81)*. These connections readily conduct water and solutes from tree to tree *(27)*. True root grafts, in contrast, are rare in aspen.

Suckers from the roots of badly decayed trees are not infected by the parent stump. Heart rot usually terminates in the base of the stump. Deteriorating clones, however, produce few suckers.

In general, sucker regeneration is proportional to the degree of cutting, with most suckers arising after a complete clearcut *(43,57,64,65,75,78)*. Typically, from 25,000 to 75,000 suckers per hectare (10,000 to 30,000/acre) are regenerated in Alaska and the Great Lakes region and about half as many in the Rockies *(28,91)*.

Light burning on heavily cut areas increases the number of suckers and stimulates their initial growth. However, hot slash fires diminish sucker vigor. Repeated burning increases stand density because it stimulates sucker numbers and prepares mineral soil seedbeds for seedling establishment; however, it reduces stand growth *(6,19,28,56,64,78)*. Surface fires in established aspen stands are not common because of aspen's inherently low flammability. When they do occur, fire wounds and loss of shallow feeder roots substantially reduce aspen productivity. Fire is a useful tool, however, to stimulate regeneration and to reduce competition if clearcutting is not practiced. It is especially valuable for regenerating deteriorated stands and for maintaining wildlife habitat *(21,57)*.

Disking stimulates suckering, but sucker growth and survival are usually diminished because of injury to their sustaining parent roots. Rows of suckers often appear along furrows prepared for planting conifers.

Herbicides have been used to kill residual trees and to increase suckering without affecting sucker growth or vigor *(19,57,78)*.

Dormant season cutting generally produces vigorous suckers the next growing season. Summer cutting produces a sparse stand initially, but the number of suckers after 2 years is usually the same regardless of cutting season *(15)*. Suckering sometimes fails inexplicably after harvesting aspen on fine-textured soils during the growing season *(59)*.

The number of suckers following cutting increases as stocking density of the parent stand increases up to full site utilization. The effect of age and site index on aspen suckering is not clear *(35,81)*.

Age of wood is the most important factor in rooting quaking aspen cuttings. With rare exceptions, the species roots poorly from woody stem cuttings even when treated with indolebutyric acid (IBA). However, newly initiated shoots can usually be induced to root by dipping in IBA or other commercially available rooting powders. These softwood stem cuttings should be taken from actively growing shoots except during the period of extremely rapid mid-season elongation *(14,63,78)*. Propagation by excising succulent young sucker shoots from root cuttings is easily accomplished by treating the shoots with IBA and growing them in a suitable medium in a misting chamber until rooted, in about 2 to 3 weeks *(62)*. Quaking aspen scions can be grafted onto balsam poplar (*Populus balsamifera*), willows (*Salix* spp.), or bigtooth aspen (*P. grandidentata*). Quaking aspen plantlets have been produced by tissue culture *(81)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Quaking aspen is a small- to medium-sized, fast-growing, and short-lived tree. Under the best of conditions, however, it may attain 36.5 m (120 ft) in height and 137 cm (54 in) in d.b.h. The current national champion is 114 cm (45 in) d.b.h. and 26 m (86 ft) tall near Fort Klamath, OR. More typically, mature stands may range from 20 to 25 m (66 to 82 ft) tall and average 18 to 30 cm (7 to 12 in) d.b.h. A few vigorous trees attain a maximum age of about 200 years (oldest recorded is 226 years) in Alaska and the Rocky Mountain region *(28,42)*. Although individual ramets of a clone may be short lived, the clone may be thousands of years old *(46)* and longer lived than the oldest giant sequoia (*Sequoiadendron giganteum*).

The tallest quaking aspen are found in a belt bordering the midcontinental prairie region at about latitude 55° N., and in north-central Minnesota, northern Michigan, and in the Southwest. Few quaking aspen exceed 26 or 27 m (85 to 90 ft) in Alaska *(38)*.

Growth and decay are both generally slower in Alaska and the West than in the East, hence pathological rotations are longer—80 to 90 years in Utah and 110 to 120 years for Colorado and Wyoming. In northern Minnesota, the pathological rotation is about 55 to 60 years and even shorter in southern Wisconsin and Michigan *(35,69,70)*.

Now and in the foreseeable future, most aspen will be extensively managed (complete clearing for site preparation, no thinning) for fiberboard, pulpwood, flakeboard, and some sawtimber. Aspen is harvested either as whole-tree chips or as bolewood to a nominal top size for pulpwood or sawtimber. Some of the very best stands can be thinned to increase the production of large bolts *(57,58)*.

Site quality varies regionally, being highest in the Lake States, followed by Alaska and the West. Biomass mean annual increment on the better sites in the Lake States and Canada culminates at about age 30 and at 4.4 to 4.8 mg/ha (2-2.2 tons/acre) dry weight *(16,60)*. Mature stands in Newfoundland typically carry 64 m^2/ha (280 ft^2/acre) basal area. This amounts to 376 mg/ha (167 tons/acre) at age 90 years, or 4.2 mg/ha/yr (1.9 tons/acre/year) *(54)*. However, exceptionally good growth of quaking aspen is possible in Arizona and in Colorado and southern Wyoming *(44,70)*. A natural triploid clone in Minnesota produced an annual yield of 14.6 m^3/ha (208 ft^3/acre) of bolewood over 38 years *(59)*.

Aspen responds to intensive management. Production by thinned stands for a 50-year rotation, including thinnings removed at ages 10, 20, and 30, is about 511 m^3/ha (7,300 ft^3/acre), or 10.2 m^3/ha (146 ft^3/acre) per year. This is about 42 percent greater than for similar, but unthinned, stands *(58)*. Quaking aspen growth can be further increased by fertilization and irrigation *(24,26,29,59,84)*. Sub-optimal fiber yield and the threat of *Armillaria mellea* root rot limit the practicality of rotations shorter than 15-20 years *(77)*.

Rooting Habit—Seedlings initially have a short taproot, but a heart root system develops on deep, well-drained soils. Clonal ramets have a flat root system when young but again will develop a heart system on deep, well-drained soils. If rooting depth is restricted, a flat root system develops regardless of regeneration origin *(28,59)*.

The shallow and extensive laterals have cordlike branch roots that undulate and meander for great distances without tapering. These roots are the main producers of suckers, particularly when they are close to the soil surface. Roots tend to follow soil surface irregularities and may even grow into decaying stumps or logs. The fine feeding roots are found at all levels down to 0.6 to 0.9 m (2 to 3 ft) except in restrictive horizons. Sinker roots occur as frequently as every meter or so on the lateral roots. They may descend to depths of 3 m (10 ft) or more where they end in a dense fan-shaped fine root mass. Sinkers are capable of penetrating strongly massive soil horizons or cracks in bedrock and often use vacated root channels *(28,78)*.

Reaction to Competition—In both the eastern and western parts of its range, quaking aspen is classed as very intolerant of shade, a characteristic it retains throughout its life. Natural pruning is excellent, and long, clean stems are usually produced when side shade is present. However, this is a clonally variable characteristic and self-pruned and unpruned clones exist side by side in some stands *(69,78)*. The intolerance of aspen to shade dictates an even-aged silvicultural system, that is, clearcutting, for regenerating fully stocked sucker stands and maximizing growth *(19,57,75)*.

The tree has a pronounced ability to express dominance, and overstocking to stagnation of growth is extremely rare.

Quaking aspen is an aggressive pioneer. It readily colonizes burns and can hold invaded land even though subjected to fires at intervals as short as 3 years. In the northeastern United States, it is an old-field type, and in Canada it invades grassland if fire is excluded. In the Central Rocky Mountains, it constitutes the typical fire climax at the lower elevations of the subalpine forest. The extensive stands of aspen in that area are usually attributed to repeated wildfires, and aspen is generally regarded as a successional species able to dominate a site until replaced by less fire-enduring but more shade-tolerant conifers, a process that may take only a single aspen generation or as long as 1,000 years of fire exclusion. Aspen is considered a permanent type on some sites in the intermountain region of Utah, Nevada, and southern Idaho, but conifers would invade the type if seed trees were available.

The uneven-aged character of some western aspen stands suggests that under certain conditions aspen is self-perpetuating without major disturbance. These stands are relatively stable and can be considered *de facto* climax. Seral and stable aspen stands seem to be associated with certain indicator species *(28,78,82)*.

In its eastern range, aspen in the absence of disturbance is regarded as transient. Successional patterns are determined by soil water regime *(61)*. Pure aspen stands gradually deteriorate to a "shrubwood" dominated by the shrub component of the stand and with only a few scattered aspen suckers. If intolerant associates are present, they will outlive the aspen and eventually dominate but in turn will be replaced again by the shrubwood type. If tolerant hardwoods or balsam fir *(Abies balsamea)* are associated with aspen, they will eventually dominate by their longevity and ability to regenerate in their own shade *(81)*.

The deterioration of aspen stands begins earliest at the southern limits of its eastern range and seems to be related to summer temperatures. Deterioration begins when crowns in old stands can no longer grow fast enough to fill the voids in the canopy left by dying trees. Increased breakage accelerates the deterioration process, which may be completed in as few as 3 or 4 years *(81)*. Deterioration is a much slower process in the West, where aspen often is replaced by conifers. Dry sites may revert to rangeland dominated by shrubs, forbs, and grasses. Sometimes suckers appear in a deteriorating stand and ultimately an all-age climax aspen forest develops *(28)*.

Damaging Agents—Numerous factors other than competition injure or kill young stands *(25,40)*. Young trees are sometimes killed by bark-eating mammals, such as meadow mice and snowshoe hares, which may girdle the stem at or near the ground line. Also, larger animals, such as mule deer, white-tailed deer, elk, and moose, frequently seriously damage reproduction by browsing and by rubbing their antlers against the stems. Elk and moose can also damage pole- and saw log-size trees by "barking" them with their incisors. Such injuries often favor secondary attack by insects or pathogens. Heavy use by overwintering big game animals can greatly reduce the number of aspen trees in localized areas. Cattle and sheep browsing is a serious problem in many areas of the Rockies because livestock are allowed to range through recent aspen clearcuts. Mature aspen stands adjacent to livestock concentrations (water holes, salt blocks, isolated stands in large open areas) often have root damage, are declining, and have few if any suckers present. Excessive use and vandalism by recreationists has caused aspen to deteriorate in many campsites *(41,70)*.

Beaver feed on the young tender bark and shoots of aspen and often cut down large numbers of trees near their colonies. A high population of porcupines can greatly damage tree crowns both directly by feeding, and indirectly by increasing the trees' susceptibility to attack by insects and diseases.

The red-breasted and yellow-bellied sapsuckers may seriously scar trees with drill holes. Minor damage is caused by such woodland birds as the ruffed grouse and the sharp-tailed grouse, which feed on the buds of quaking aspen; ruffed grouse also feed on the leaves during the summer months *(78)*.

Aspen is susceptible to a large number of diseases *(28,39,41,81,82)*. Shoot blight of some aspen caused by *Venturia macularis* is periodically severe. Angular black spots appear on the leaves, enlarging until the leaf dies. If the infection occurs at the top of the tree, the entire new shoot may be infected, blackened, killed, and bent to form a "shepherd's crook." This disease is common in young stands. A similar leaf disease in Wisconsin is caused by *Colletotrichum gloeosporioides*.

Two or more species of *Ciborinia* cause a leaf spot on trees of all ages. When the disease is severe, small trees may be killed, but older ones rarely die. *Marssonina populi* causes a leaf spot and shoot blight that is especially prevalent and damaging in the western states. It is responsible for occasional severe defoliation. Severe, repeated infection can cause mortality, although susceptibility to this disease varies greatly among clones. Another leaf spot of aspen is caused by *Septoria musiva*.

Several leaf rust fungi of the genus *Melampsora* infect aspen. *M. medusae* is common east of the Rocky Mountains. *M. abietis-canadensis* occurs throughout the range of eastern hemlock (*Tsuga canadensis*) and *M. albertensis* in the West. All can discolor and kill aspen leaf tissue and cause premature autumn leaf drop, but their damage is not serious.

Powdery mildew, *Erysiphe cichoracearum* in the West and the widespread *Uncinula salicis* can be conspicuous on aspen leaves but probably do little damage.

Recently, viruses have been detected in a few quaking aspen clones. Once trees in the clone are infected, regeneration by suckering maintains the infection, which is then impossible to eliminate except by artificially culturing virus-free tissue. The full extent and seriousness of viruses in aspen is unknown but decline of some clones has been attributed to them in both the East and the West.

Stain and decay have the greatest direct impact of the many stem pathogens on wood production. The role of microorganisms frequently associated with discoloration is poorly understood because staining also develops in their absence. Bacteria and yeast organisms are commonly associated with "wetwood," a water-soaked condition of live trees that leads to wood collapse during lumber drying.

A number of different bacteria and fungi are found in aspen tissue, apparently interacting to follow one another successionally, with bacteria appearing first. *Phellinus tremulae* causes a white rot of the heartwood at first but may eventually invade the entire stem. It causes the greatest volume of aspen decay and is so prevalent it conceals rot caused by other fungi. Sporophores (fruiting bodies) are the most reliable external indicator of decay. They provide a means to estimate present and future decay. Resistance to this fungus is strongly genetically controlled. Incidence and extent of infection increases with tree age or size but is not strongly related to site *(76)*.

Peniophora polygonia is the second most important trunk rot fungus in the West and in Alaska, but it causes little actual cull. *Libertella* spp. is also an important trunk rot fungus in the West. Other less important trunk rot fungi found on aspen include *Radulodon caesarius, Peniophora polygonia, P. rufa,* and *Pholiota adiposa*.

More fungi species cause butt and root rots than trunk rots—as much as one-third of the decay volume in Colorado. *Collybia velutipes* is found in Alaska and causes the greatest amount of butt cull in the West. *Ganoderma applanatum* may be as important because it also decays large roots, which leads to windthrow. Less important butt rot fungi include *Pholiota squarrosa, Gymnopilus spectabilis, Peniophora polygonia, and Armillaria mellea*. The latter is primarily a root rot which can infect a high proportion of the trees *(74)*. Other locally important root rots in the West include *Phialophora* spp. and *Coprinus atramentarius*.

Stem cankers are common diseases of aspen that have a great impact on the aspen resource. Depending on the causal fungus, cankers can kill a tree within a few years or persist for decades. Hypoxylon canker caused by *Hypoxylon mammatum* is probably the most serious aspen disease east of the Rockies, killing 1 to 2 percent of the aspen annually. It is not an important disease in the West, nor has it been found in Alaska. The infection mode of *Hypoxylon* is poorly understood but seems to be related to ascospore germination inhibitors in bark. Most canker infections seem to originate in young branches with scars or galls formed by twig-boring insects *(4)*. Once infected, the host bark tissue is rapidly invaded and the fungus girdles and kills the tree in a few years *(5)*.

Ceratocystis canker is a target-shaped canker caused by *Ceratocystis fimbriata, C. moniliformis, C. piceae, C. pluriannulata, C. ambrosia, C. cana, C. serpens, C. crassivaginata, C. populina, C. tremulo-aurea,* and *C. alba*. This canker is found throughout the range of aspen, with *C. fimbriata* the most common causal pathogen. These cankers seldom kill aspens but can reduce usable volume of the butt log. Infection is primarily through trunk wounds and insects are the primary vectors.

Sooty-bark canker of aspen is caused by *Phibalis pruinosa* and is common and a major cause of mortality in Alaska and the West. The fungus infects trunk wounds and spreads rapidly, killing trees of all sizes. The fungus has been found only as an innocuous bark saprophyte on quaking aspen in the East.

Cytospora canker is caused by *Cytospora chrysosperma*, a normal inhabitant of aspen bark. The fungus is not considered a primary pathogen and causes cankers, lesions, or bark necrosis only after the host tree has been stressed, such as by drought, fire, frost, suppression, or leaf diseases. The disease is most serious on young trees and is found throughout the range of aspen.

Dothichiza canker, caused by *Dothichiza populea*, occurs in the eastern range of aspen. It is an endemic disease of young or weakened trees and is not found in vigorous stands.

In Ontario, a canker caused by *Neofabraea populi* has been found on young aspen. Few trees have been killed by it, however, and the disease is not known in the United States.

Cryptosphaeria populina cause a long, narrow, vertical canker that may spiral around an aspen trunk for 1 to 6 m (3 to 20 ft) or more. It is common in the West as far north as Alaska. Trees with large cankers have extensive trunk rot and are frequently broken by wind.

Aspen is susceptible to three types of rough-bark which are caused by the fungi *Diplodia tumefaciens*, *Rhytidiella baranyayi*, and *Cucurbitaria staphula*. Rough, corky bark outgrowths persist for many years but do little harm.

Quaking aspen hosts a wide variety of insects *(28,81)*. One Canadian survey recorded more than 300 species, but only a few are known to severely damage trees. They may be grouped into defoliators, borers, and sucking insects.

Defoliators of aspen belong primarily to the orders Lepidoptera and Coleoptera. The forest tent caterpillar *(Malacasoma disstria)* and the western tent caterpillar *(M. californicum)* have defoliated aspens over areas as large as 259 000 km^2 (100,000 mi^2). Outbreaks usually persist for 2 to 3 years and may collapse as quickly as they begin *(88)*. Aspen growth losses during defoliation have been as high as 90 percent and may take as long as 3 or 4 years for total growth recovery. Some trees never recover and die—as much as 20 to 80 percent of them on poor sites *(90)*. On good sites mortality may be restricted to suppressed trees *(59)*.

The large aspen tortrix *(Choristoneura conflictana)* is found throughout the range of aspen. It has defoliated trees over an area as large as 25 900 km^2 (10,000 mi^2) in Canada and Alaska. Caterpillars predominantly infest the leaves of early flushing clones *(89)*. Outbreaks normally collapse in 2 or 3 years and, although aspen growth is reduced, few trees are killed.

In the East, aspen is a favored host for the gypsy moth *(Lymantria dispar)* and the satin moth *(Leucoma salicis) (78)*.

A great number of leaf tiers defoliate aspen. *Sciaphila duplex* is one that is often associated with the large aspen tortrix and has been a major pest in Utah. Other Lepidopterous defoliators of aspen include the Bruce spanworm, *Operophtera bruceata*, and *Lobophora nivigerata*.

Three species of leaf-rolling sawflies of the genus *Pontania* sometimes erupt in local outbreaks in the Lake States. *Anacampsis niveopulvella* is a Lepidopterous leaf roller that causes local damage in the West. Sawflies of the *Platycampus* genus chew holes in leaves.

The more common leaf miners of aspen are the aspen leaf miner *(Phyllocnistis populiella)*, the aspen blotch miners *(Phyllonorycter tremuloidiella* and *Lithocolletis salicifoliella)*, and a leaf-mining sawfly *(Messa populifoliella)*.

Defoliating beetles include the aspen leaf beetle *(Chrysomela crotchi)*, the cottonwood leaf beetle *(C. scripta)*, the American aspen beetle *(Gonioctena americana)*, and the gray willow leaf beetle *(Pyrrhalta decora)*. All have similar feeding habits; the larvae skeletonize lower surfaces of leaves, and adults feed on whole leaves.

Wood-boring insects that attack aspen are primarily beetles of the Cerambycidae (round-headed borers or long-horned beetles) and Buprestidae (flatheaded borers or metallic beetles). The poplar borer *(Saperda calcarata)* is the most damaging. The larvae tunnel in the bole, weakening and degrading the wood. Breakage by wind increases and the tunnels serve as infection courts for wood-rotting fungi. *S. moesta* is a smaller related borer that attacks small suckers and aspen twigs. It is important only in the West. *Xylotrechus obliteratus* has killed large areas of aspen in the West above 2130 m (7,000 ft).

The root-boring saperda *(Saperda calcarata)* feeds on phloem and outer sapwood near the base of young aspen suckers. Oviposition incisions of the poplar gall saperda *(S. inornata)* frequently cause globose galls to form on the stems of young suckers and on small branches of larger trees. These oviposition wounds can serve as infection sites for Hypoxylon that can then grow from a branch gall down into the bole of the tree causing a canker *(4)*. The poplar branch borer *(Oberea schaumi)* attacks larger suckers and tree limbs. Damage by all these insects can lead to stem breakage. Site quality is not an important variable, and maintaining high stocking density of vigorous suckers is the best practice to minimize loss.

Two flatheaded borers, the bronze poplar borer *(Agrilus liragus)* and the aspen root girdler *(A. horni)*, bore galleries that disrupt nutrient and water movement. The former attacks sucker stems and makes zig-zag galleries; the latter girdles the sucker with a spiral gallery from the lower trunk to the roots and back. *A. anxius* also girdles and kills aspen twigs in the West.

Some other Buprestids attacking aspen in the East are the flatheaded apple tree borer *(Chrysobothris femorata)*, the Pacific flatheaded borer *(C. mali)*, and the flatheaded aspen borers *(Dicerca tenebrica, D. divaricata*, and *Poecilonota cyanipes)*. The first two and the latter are also reported in the West, along with the aspen ambrosia beetle (*Trypodendron retusum*). None of these cause serious injury in well-managed stands.

A widespread weevil, the poplar and willow borer, *Cryptorhynchus lapathi*, can riddle aspen stems with galleries, especially planted trees.

A clearwing moth of the genus *Aegeria*, and willow shoot sawfly (*Janus abbreviatus*) are examples of borers from nonbeetle families.

In the West, the fungus *Ceratocystis fimbriata* is carried by *Epurea* spp., *Nudobius* spp., and *Rhisophagus* spp. (*28*).

Sucking insects are represented mainly by aphids and leafhoppers. The poplar vagabond aphid (*Mordvilkoja vagabunda*) causes a peculiar curled and twisted gall of leaves as large as 5 cm (2 in) in diameter at the tip of twigs. Poplar petiole gall and twig gall aphids of the genus *Pemphigus* produce swellings on leaf petioles. Increased forking of aspen suckers may be caused by high populations of the speckled poplar aphid (*Chaitophorus populicola*) and the spotted poplar aphid (*Aphis maculatae*). They are commonly found on expanding aspen sucker leaves (*35,81*).

The genera *Idiocerus*, *Oncomtopia*, *Macropsis*, *Oncopsis*, and *Agallia* have several species of leafhoppers that cause leaf browning and slitlike ruptures in the bark of twigs. Only *Idiocerus* spp. have been found in the West. Several species of scale insects such as the oystershell scale (*Lepidosaphes ulmi*) are found on aspen but do little damage to healthy trees. Cutworms (moth family Noctuidae larvae) sometimes can cut a large number of succulent new suckers at the ground line. Black carpenter ants (*Camponotus pennsylvanicus*) frequently use and extend the tunneling made by the poplar borer, causing further damage (*35,78*).

Aspen is highly susceptible to fire damage. Fires may kill trees outright or cause basal scars that serve as avenues of entrance for wood-rotting fungi. Intense fires can kill or injure surface roots and thereby reduce sucker regeneration (*19,56,78*).

Early spring frosts may kill new leaves and shoots and, when especially severe, some of the previous year's shoots. Overwinter freezing can cause frost cracks. Strong wind can uproot or break mature aspen and even moderate wind can crack the bole of trees with lopsided crowns. Hail can bruise the bark of young aspen and, in severe storms, kill entire sapling stands. Aspen suffers little from ice storms or heavy wet snow, except when in leaf. Snow creep on steep slopes can bend or break aspen suckers as tall as 1.2 m (4 ft) (*28*).

Aspen suddenly exposed to full sunlight may suffer sunscald. Pole-size trees are more susceptible than saplings (*19,58*).

Aspen growth and vigor suffer from drought (*79*), and drought-stressed trees become predisposed to secondary agents such as insects and disease. Mechanical injuries inflicted on aspen bark by thoughtless recreationists can lead to infection by canker disease and eventual death in as few as 10 to 20 years.

Special Uses

Aspen provides habitat for a wide variety of wildlife needing young forests, including hare, black bear, deer, elk, ruffed grouse, woodcock, and a number of smaller birds and animals. Ruffed grouse use all age classes of aspen—sapling stands for brooding, pole stands for overwintering and breeding, and older stands for nesting cover and winter food (*53,55,67,68*).

Aspen forests allow more water or ground water recharge and streamflow than do conifer forests. This is primarily due to lower seasonal water losses to interception and transpiration by aspen compared to conifers (*34*). Clearcutting the aspen type may increase streamflow by as much as 60 percent during the first year. Subsequently, water yields gradually decline to preharvest levels and stabilize when maximum leaf area is attained at about age 10 to 25 (*53*).

The aspen type is esthetically appealing. The light bark and autumn colors are a pleasing contrast to dark conifers. In the West in particular, the type is used by recreationists during all seasons of the year.

Aspen stands produce abundant forage—as much as 1100 to 2800 kg/ha (1,000 to 2,500 lb/acre) in the Rockies annually, or three to six times more than typical conifer stands. These amounts are comparable to forage production on some grasslands. Although the type is sought after for summer sheep and cattle range in the West, its use for grazing in the East is much more limited (*28*).

Aspen stands, because of low fuel accumulations, are low in flammability and make excellent firebreaks. Violent crown fires in conifers commonly drop to the ground and sometimes are even extinguished when they reach an aspen stand (*28*).

Whole-tree aspen chips can be processed into nutritious animal feed ("Muka") or biomass fuels (*82*). Aspen could be grown for such purposes in dense sucker stands on biological rotations of 26 to 30 years (*16*).

Wood products from aspen include pulp, flakeboard, particleboard, lumber, studs, veneer, plywood, excelsior, shingles, novelty items, and wood flour. Aspen makes particularly good sauna benches and playground structures because the wood surface does not splinter.

Genetics

The vegetative cells of aspen, as well as those of nearly all aspen hybrids, contain 19 pairs of chromosomes. A number of triploid aspen (with three sets of chromosomes rather than the normal two) have been located in Utah, the Lake States, and Colorado. A few albino aspen seedlings have been observed, as have two albino aspen suckers, which were thought to result from a somatic mutation in aspen root tissue *(30,37,78)*.

Population Differences and Races

In aspen, the clone is the biological entity—a multistemmed individual that may be thousands of years old *(46)*. The ability to propagate by root suckers assures genetic uniformity and adaptation to the present environment *(73)*. Despite the great genetic variability among clones and the virtually infinite amount of genetic recombination in the billions of seed produced, the chance for expression of this recombination and further adaptive change in established seedlings is very small *(6)*. Stands that are clearcut or destroyed by fire or windstorms may provide some microsites suitable for seedling establishment. However, seedlings are not likely to compete successfully with the faster growing root suckers that are also regenerated under such circumstances *(93)*.

By definition, intraclonal genetic variability does not exist (except by somatic mutation), but interclonal variation is great on a local and regional level. Populations of aspen have undergone selection leading to better adaptation to local environments. Its extensive north to south range has induced strong racial variation along latitudinal and elevational gradients. In one study, seedlings from Saskatchewan ceased growing at a longer day-length and had heavier root systems than seedlings from Wisconsin *(78)*. Another study found that local southeastern Michigan seedlings grew faster and later into the season than quaking aspen from more northerly or higher altitude sources *(20)*.

Hybrids

Quaking aspen is known to hybridize naturally with the following species (hybrid names and authors are given in parentheses):

Populus alba (*P.* × *heimburgeri* Boivin)
P. angustifolia (*P.* × *senni* Boivin)
P. balsamifera (*P.* × *dutillyi* Lepage)
P. balsamifera × *deltoides*
  (*P.* × *polygonifolia* Barnard)
P. deltoides (*P.* × *bernardii* Boivin)
P. grandidentata (*P.* × *smithii* Boivin,
  P. × *barnesii* W. H. Wagner) *(49)*.

Natural hybrids between *P. tremuloides* and *P. grandidentata* have been reported in lower Michigan, Massachusetts, and Canada *(8,13,78)*. Such hybrids are moderately fertile, and backcrosses with parent species are possible *(13)*. Many backcross individuals are indistinguishable between *P. tremuloides* or *P.* × *smithii* so the true extent of hybridization, backcrossing, and gene flow between these native aspens is difficult to determine *(31)*.

Natural hybrids between the European *Populus alba* and *P. tremuloides* have been reported from Michigan *(8)* and occur in a number of localities in the vicinity of Ottawa, ON *(78)*. This cross produces viable seed, as does a cross of *P.* × *canescens* (Ait.) Sm. with *P. tremuloides*.

Populus tremuloides also crosses readily with *P. tremula* L., the European aspen. Crosses between diploid *P. tremuloides* females and a tetraploid male *P. tremula* from Sweden have produced triploid progeny with exceptionally improved growth. Numerous other artificial crosses have been made but only *P. tremuloides* × *davidiana* Dode (Asiatic aspen) has shown much promise for commercial use. Little intraspecific breeding of quaking aspen has been done *(7,78,81)*.

One particularly important limitation of almost all quaking aspen inter- and intraspecific hybrids is that rooting progeny asexually by woody stem cuttings is extremely difficult. Other *Populus* that root easily in this manner have a decided advantage for mass-producing inexpensive and easily handled planting stock. Nevertheless, *P. tremuloides*, *P. tremula*, and their hybrids can be propagated commercially by culturing meristematic explants from buds *(1)*.

P. tremuloides is more closely related to *P. tremula* than to *P. grandidentata* *(12)*.

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Populus trichocarpa Torr. & Gray **Black Cottonwood**

Salicaceae **Willow family**

Dean S. DeBell

Black cottonwood *(Populus trichocarpa)* is the largest of the American poplars and the largest hardwood tree in western North America. Known also as balsam cottonwood, western balsam poplar, and California poplar, it grows primarily on moist sites west of the Rocky Mountains. The most productive sites are the bottom lands of major streams and rivers west of the Cascade Range in the Pacific Northwest. Pure stands may form on alluvial soils. Black cottonwood is harvested and used for lumber, veneer, and fiber products. Many kinds of wildlife use the foliage, twigs, and buds for food, and the tree is planted for shade and in windbreaks and shelterbelts.

Habitat

Native Range

The range of black cottonwood (fig. 1) extends northeast from Kodiak Island along Cook Inlet to latitude 62° 30′ N., then southeast in southeast Alaska and British Columbia to the forested areas of Washington and Oregon, to the mountains in southern California and northern Baja California (lat. 31° N.). It is also found inland, generally on the west side of the Rocky Mountains, in British Columbia, western Alberta, western Montana, and northern Idaho. Scattered small populations have been noted in southeastern Alberta, eastern Montana, western North Dakota, western Wyoming, Utah, and Nevada.

Climate

Populations of black cottonwood grow in climates varying from relatively arid to humid, but best growth is attained in the humid coastal forests of the Pacific Northwest *(23)*. Annual precipitation ranges from 250 mm (10 in) to more than 3050 mm (120 in). Only about one-third of the annual precipitation occurs during the growing season, and in mountainous and inland areas much of the dormant-season precipitation falls as snow. The frost-free period ranges from about 70 days in the interior areas to more than 260 days in southern California. Maximum temperatures range from 16° to 47° C (60° to 117° F); minimum temperatures, from 0° to -47° C (32° to -53° F).

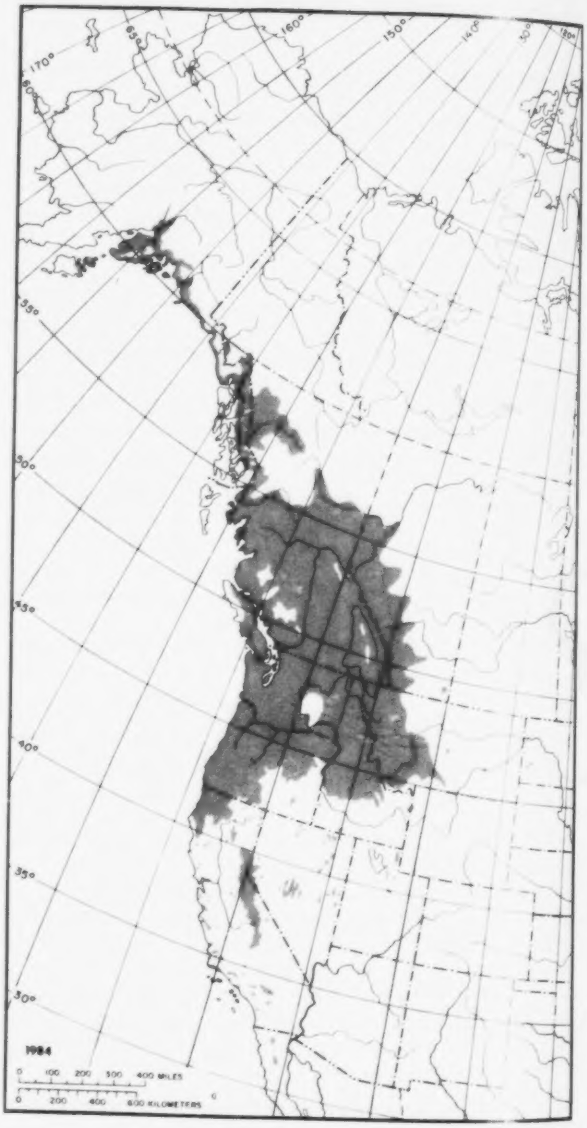

Figure 1—*The native range of black cottonwood.*

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Soils and Topography

Black cottonwood grows on a variety of soils and sites, from moist silts, sands, and gravels of islands and new river bars to rich humus soils, loams, and occasionally clay soils of upland sites *(23)*. The most extensive black cottonwood stands are on soils of the order Entisols; the species also is common on Inceptisols and occasionally may be present on soils of other orders. High soil acidity (low pH) may restrict occurrence of black cottonwood on fine-textured soils where other site factors are favorable *(9)*. Studies in British Columbia *(27)* have indicated that abundant moisture, nutrients, oxygen, and nearly neutral soil reaction (pH 6.0 to 7.0) are required for optimum production. Growth is best at low elevations on deep, moist alluvial soils, but some upland soils are productive cottonwood sites *(27)*. The latter include loessial soils of high nutrient status in areas of abundant rainfall.

Black cottonwood grows from sea level to 600 m (2,000 ft) on the Kenai Peninsula of Alaska and up to 1500 m (5,000 ft) in the Cascade Range of Washington *(23)*. In British Columbia, the elevation range extends to nearly 2100 m (7,000 ft) in the interior valleys of the Selkirk Range. In central and eastern Washington, as well as other dry areas, the species is usually limited to protected valleys and canyon bottoms, along stream banks and edges of ponds and meadows, and to moist toe slopes.

Associated Forest Cover

Black cottonwood often forms extensive stands on alluvial sites at low elevations along the Pacific coast. Arborescent willows are its major associates in two cover types *(3)*: Black Cottonwood–Willow (Society of American Foresters Type 222) and Cottonwood–Willow (Type 235). In the latter type, balsam poplar *(Populus balsamifera)* is the dominant cottonwood. Major willow species are Pacific *(Salix lasiandra)*, northwest *(S. sessilifolia)*, river *(S. fluviatilis)*, and Scouler *(S. scouleriana)* willow *(4)*. In other coastal forests, black cottonwood grows in mixture with red alder *(Alnus rubra)*, Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, western redcedar *(Thuja plicata)*, Sitka spruce *(Picea sitchensis)*, grand fir *(Abies grandis)*, bigleaf maple *(Acer macrophyllum)*, Oregon ash *(Fraxinus latifolia)*, black hawthorn *(Crataegus douglasii)*, and several birch *(Betula* spp.) and cherry *(Prunus* spp.) species. Associates in interior forests may include western white pine *(Pinus monticola)*, ponderosa pine *(P. ponderosa)*, white fir *(Abies concolor)*, western larch *(Larix occidentalis)*, subalpine fir *(A. lasiocarpa)*, white spruce *(Picea glauca)*, Engelmann spruce *(P. engelmannii)*, and quaking aspen *(Populus tremuloides)*.

Shrub species associated with black cottonwood include vine maple *(Acer circinatum)*, red-osier dogwood *(Cornus stolonifera)* and other *Cornus* spp., beaked hazel *(Corylus cornuta)*, Nootka rose *(Rosa nutkana)*, thimbleberry *(Rubus parviflorus)*, salmonberry *(R. spectabilis)*, elder *(Sambucus* spp.), bearberry honeysuckle *(Lonicera involucrata)*, spirea *(Spiraea* spp.), and common snowberry *(Symphoricarpos albus)*.

Herbaceous associates include swordfern *(Polystichum munitum)*, lady fern *(Athyrium filix-femina)*, horsetail *(Equisetum* spp.), stinging nettle *(Urtica dioica)*, hedge nettle *(Stachys* spp.), false solomons-seal *(Smilacina stellata)*, Canada violet *(Viola canadensis)*, jewelweed *(Impatiens* spp.), enchanters nightshade *(Circaea alpina)*, golden-saxifrage *(Chrysosplenium* spp.), buttercup *(Ranunculus* spp.), bittercress *(Cardamine* spp.), angelica *(Angelica* spp.), loosestrife *(Lysimachia* spp.), bedstraw *(Galium* spp.), and iris *(Iris* spp.).

Presence of some of these understory species provides an indication of site quality in British Columbia *(27)*. Good black cottonwood sites are characterized by salmonberry, nettles, swordfern, and lady fern, as well as vigorous growth of beaked hazel and elder. On medium sites, red-osier dogwood, bearberry honeysuckle, common snowberry, and sometimes thimbleberry and Nootka rose are common. Poor sites are commonly subject to prolonged flooding, and horsetails are dominant.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Black cottonwood is normally dioecious; male and female catkins are borne on separate trees. The species reaches flowering age at about 10 years *(25)*. Flowers may appear in early March to late May in Washington and Oregon, and sometimes as late as mid-June in northern and interior British Columbia, Idaho, and Montana. Staminate catkins contain 30 to 60 stamens, elongate to 2 to 3 cm (0.8 to 1.2 in), and are deciduous. Pistillate catkins at maturity are 8 to 20 cm (3.2 to 8 in) long with rotund-ovate, three carpellate subsessile fruits 5 to 8 mm (0.20 to 0.32 in) long. Each capsule contains many minute seeds with long, white cottony hairs.

Seed Production and Dissemination—The seed ripens and is disseminated by late May to late

June in Oregon and Washington, but frequently not until mid-July in Idaho and Montana *(23)*. Abundant seed crops are usually produced every year. Attached to its cotton, the seed is light and buoyant and can be transported long distances by wind and water. Although highly viable, longevity of black cottonwood seed under natural conditions may be as short as 2 weeks to a month. There is some evidence, however, to suggest a somewhat longer lifespan under apparently adverse conditions. With proper drying and cold storage, viability and capacity to germinate can be maintained for at least 1 year *(25)*.

Seedling Development—Moist seedbeds are essential for high germination *(23)*, and seedling survival depends on continuously favorable conditions during the first month *(25)*. Wet bottom lands of rivers and major streams frequently provide such conditions, particularly where bare soil has been exposed or new soil laid down. Germination is epigeal. Black cottonwood seedlings do not usually become established in abundance after logging unless special measures are taken to prepare the bare, moist seedbeds required for initial establishment *(23)*. Where seedlings become established in great numbers, they thin out naturally by age 5 because the weaker seedlings of this shade-intolerant species are suppressed *(23)*.

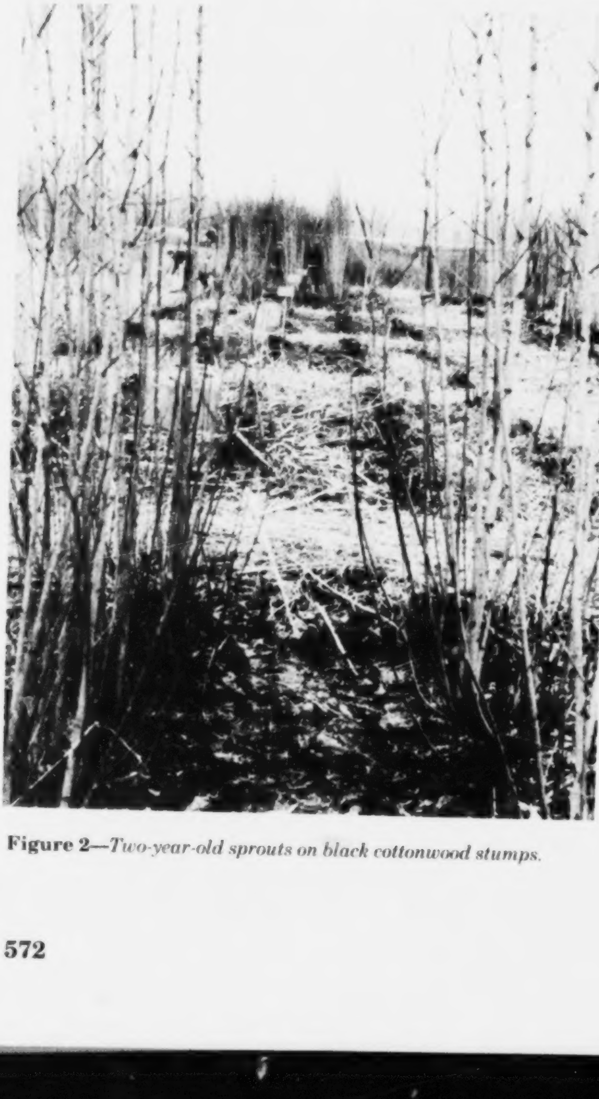

Figure 2—*Two-year-old sprouts on black cottonwood stumps.*

Vegetative Reproduction—Black cottonwood sprouts readily from stumps (fig. 2), and in one study, satisfactory coppice reproduction was obtained four times in 2-year cutting cycles *(8)*. After logging operations, black cottonwoods sometimes regenerate naturally from rooting of partially buried fragments of branches *(9)*. Sprouting from roots has also been reported *(23)*. The species also has the unusual ability to abscise small shoots complete with green leaves *(6)*. These shoots drop to the ground and may root where they fall or may be dispersed by water transport. In some situations, abscission may be one means of colonizing exposed sandbars.

The species is easily reproduced by rooted and unrooted cuttings *(30)*. The cuttings are made in the dormant season and may be as short as 15 cm (6 in). Most research and small-scale operational plantings have been established with unrooted stem cuttings taken from 1- and 2-year-old wood, 1 to 3 cm (0.4 to 1.2 in) in diameter at the small end and 40 to 60 cm (16 to 24 in) long. Good results have also been obtained with branchwood cuttings, in some instances collected from trees as old as 30 years *(9)*. Usually the cuttings are planted in the spring to a depth of 30 to 40 cm (12 to 16 in). Best establishment and growth are achieved when cuttings have healthy axillary buds, at least one of which remains above ground after planting *(22)*. Plantings of very long cuttings (3 m or 10 ft or more in length) have sometimes been used successfully to overcome problems of weed competition or animal damage *(29)*; in other cases, they have failed, presumably because top growth and thus transpiration stress outstripped root growth and the ability of the root system to provide moisture during the dry summer. The proportion of trees with poor form and the magnitude of crookedness are greater in trees established with long cuttings than with short cuttings *(10)*. Height of trees established from cuttings has frequently exceeded 1.5 m (5 ft) at the end of the first year and 6 m (20 ft) after 4 years *(11)*. Height growth rates of cottonwood sprouts have been even greater.

Sapling and Pole Stages to Maturity

Growth and Yield—Black cottonwood may attain pulpwood size in 10 to 15 years, and saw log-size trees have been observed in plantations less than 25 years old in British Columbia and Washington. For example, dominant and codominant trees of 17 cm (6.7 in) in d.b.h. and 14.8 m (48.5 ft) in height at 9 years have been reported for a good moist site *(26)*. In the lower Fraser River Valley of British Columbia, planted black cottonwoods averaged 20 cm (8 in) in d.b.h. and 16.8 m (55 ft) in height at 10 years, and some individual trees were more than 30 cm (12 in) in d.b.h. and 21.3 m (70 ft) in height *(29)*. Growth is considerably less in northerly and interior locations. In the Willamette Valley of Oregon, black cottonwood matures in 60 years or less *(23)*, but studies in British Columbia show that the species grows well for as long as 200 years *(33)*. Exceptional trees have attained 180 to 300 cm (72 to 120 in) in d.b.h. and more than 60 m (200 ft) in height *(7,35)*.

Table 1—Characteristics of natural stands of black cottonwood by site class (adapted from data collected by the British Columbia Forest Service) and summarized by Smith *(30)*

Site class and stand age		Average d.b.h.	Stocking	Height[1]	Net volume	Maximum mean annual increment	Age of culmination
	yr	*cm*	*trees/ha*	*m*	*m³/ha*	*m³/ha*	*yr*
I,	112	46	294	41.1	302.3	5.5	62
II,	101	33	415	29.6	219.9	2.8	78
III,	87	28	474	21.3	122.8	1.7	96
	yr	*in*	*trees/acre*	*ft*	*ft³/acre*	*ft³/acre*	*yr*
I,	112	18	119	135	4,319	79	62
II,	101	13	168	97	3,141	40	78
III,	87	11	192	70	1,755	24	96

[1] Dominants and codominants.

Growth and yield data for natural black cottonwood stands are available for the Quesnel region and Skeena River Valley of British Columbia *(33)*. Other Canadian studies have indicated that three site quality classes developed for German poplar *(16)* are satisfactory for black cottonwood stands in British Columbia *(30)*. The Forest Inventory Branch of the British Columbia Forest Service has collected much growth and yield data on natural stands of black cottonwood. Some of this information is summarized in table 1. These data clearly indicate that differences in yield among site classes are large; the mean annual production of site I is nearly twice that of site II, and more than three times that of site III.

Yields from black cottonwood plantations are expected to be much higher than yields from natural stands. Data from three plantations in the lower Fraser River Valley indicate mean annual increments ranging from 10.5 to 15.4 m³/ha (150 to 220 ft³/acre) per year *(28)*. A plantation established on a deep alluvial soil in coastal Washington has produced more than 500 m³/ha (7,242 ft³/acre) in 24 years (fig. 3) *(19)*. Dominant trees range from 35 to 37 m (115 to 122 ft) in height and 33 to 41 cm (13 to 16 in) in d.b.h.

Rooting Habit—Planted cuttings of black cottonwood root very well; they produce deep and widespread root systems if growth is not restricted by adverse soil conditions. Little information on rooting has been collected in natural or seedling stands.

Reaction to Competition—Black cottonwood is classed as very intolerant of shade. It grows best in full sunlight. On moist lowland sites, it makes rapid initial growth and thereby survives competition from slower growing associated species.

Data from British Columbia indicate that black cottonwood trees can take advantage of wide initial spacing *(1)*; diameters of trees and sets established at a 9.14-m (30-ft) spacing averaged 30 to 75 percent greater than those of plants established at a 1.82-m (6-ft) spacing *(28,29)*. Results from a spacing trial in Washington, however, indicate better height and diameter growth at 3.7- by 3.7-m (12- by 12-ft) spacing than at 3.0- by 9.1-m (10- by 30-ft) and 6.1- by 9.1-m (20- by 30-ft) spacings *(10)*. Black cottonwood responds well to thinning *(29)*.

In the past decade, most of the research on black cottonwood has focused on use of the species in short-rotation, coppice systems for fiber and energy. Spacings have varied from 0.3 by 0.3 m (1 by 1 ft) to 1.8 by 1.8 m (6 by 6 ft) and rotations or cutting cycles of 2 to 8 years *(8,11,12,14)*. Mean annual production has ranged from about 2 to more than 16 mg/ha (1

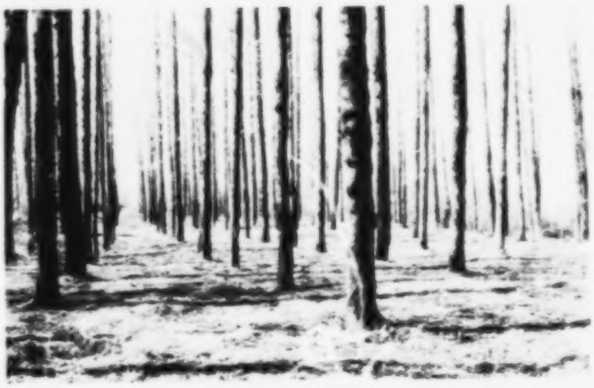

Figure 3—*A 24-year-old black cottonwood plantation in coastal Washington with 720 stems per hectare (291/acre) and mean annual volume increment of about 21.1 m³/ha (302 ft³/acre).*

to 7 tons/acre). The most recent findings suggest that rotations longer than 4 years (perhaps 8 or more) result in highest mean annual production *(11)*; with such rotations, spacings of 1.8 by 1.8 m (6 by 6 ft) or wider may be used, provided that competition from grass and weeds is controlled. Higher coppice yield was obtained in a mixed planting of black cottonwood and red alder (a nitrogen-fixing species) than from pure plantings of either species *(2)*. A subsequent study of the black cottonwood-alder mixture on a better site showed no benefits after the second year, presumably because cottonwood shaded and overtopped alder and thus impaired nitrogen fixation *(13)*.

Damaging Agents—Young saplings are frequently injured and sometimes killed by unseasonably early or late frosts *(23)*. Frost cracks also lower quality of wood and provide an entrance for decay fungi *(30)*. Ice storms and heavy snowfall cause considerable breakage and permanent bending *(29)*. Wind damage is common, especially in stands where black cottonwood trees are much taller than surrounding vegetation; top breakage and bending result. Erosion along rivers and major streams also takes its toll in adjacent black cottonwood stands. The species is highly susceptible to fire damage.

Mammals can create serious problems in black cottonwood plantations, especially at time of establishment or soon after. Meadow voles and meadow mice can cause severe losses in young plantations; such damage occurs most commonly on grassy or herb-covered sites. The voles feed on roots and sometimes girdle the lower stem. In some locations, rabbits and hares cause losses in young cottonwoods via clipping and basal girdling damage. Damage also results when beavers use cottonwood for food and construction of dams. Browsing and trampling of saplings by elk and deer sometimes decimate small, isolated plantings. Slugs have girdled cottonwood stems and presumably have eaten buds and newly emergent leaves of recently planted cuttings in the lower Columbia River valley.

Although several insects attack black cottonwood *(5,17)*, none has yet been reported as a pest of economic significance. Foliar feeders include tent caterpillars *(Malacosoma* spp.), two sawflies *(Phyllocolpa bozemanii* and *Nematus currani)*, the satin moth *(Leucoma salicis)*, and a leaf blotch miner *(Agromyza albitarsis)*. Oystershell scale *(Lepidosaphes ulmi)* was reported as frequently killing twigs and branches, and sometimes a whole tree. A bud midge *(Contarinia* spp.) caused considerable injury to buds of stressed trees (e.g., nursery-grown trees that have been transplanted, and trees on dry sites or in dry years) *(9)*. A small bark moth *(Laspeyresia populana)* mines the cambium of the trunk and larger branches. Two borers feed under the bark and in the wood, a flatheaded borer *(Poecilonota montana)* and the poplar-and-willow borer *(Cryptorhynchus lapathi)*. The latter is a European insect that is now established throughout much of the range of black cottonwood and has caused some damage in cottonwood plantings. Other flatheaded and roundheaded borers and ambrosia beetles are known to destroy the wood of black cottonwood.

At least 70 fungal species cause decay in cottonwood, but only six fungi cause significant losses in British Columbia; two of these *(Spongipellis delectans* and *Pholiota destruens)* cause 92 percent of the loss *(15,17,33)*. A leaf rust *(Melampsora* spp.) has been observed in young plantations, and susceptibility to the rust appears to vary greatly across the geographic range of the species. This disease limits photosynthesis and causes leaves to fall prematurely, thereby decreasing tree growth and vigor. Severe *Melampsora* infections have been observed when clonal material from relatively dry areas (e.g., east of the Cascade Range in Washington or Oregon and northern California) was planted in western Washington *(9)*; in one instance, such infections resulted in death of the clones. Other foliage diseases include leaf-spot syndrome *(Venturia populina)* and yellow-leaf blister *(Taphrina populisalicis)*. A deformity of catkins is caused by *Taphrina johansonii*. Cytospora canker *(Cytospora chrysosperma)* is widespread under forest conditions but rarely causes significant damage in vigorous cottonwood stands. It may cause problems, however, to cuttings in nurseries and plantations. Stem cankers in various areas have been reported as caused by *Dothichiza populea*, *Fusarium* spp., *Hypoxylon mammatum*, *Nectria galligena*, and *Septoria musiva*. None appear to be of great significance in management of black cottonwood, but severe attacks of a bacterial canker have reportedly limited planting of the species in Europe. Black cottonwood is also subject to the condition known as wet wood, which leads to wood collapse during drying.

Special Uses

Black cottonwood has been planted as windbreaks and shelterbelts in conjunction with irrigated agriculture in the Columbia River basin.

The wood of black cottonwood is similar to that of other cottonwoods *(20,34)*. It has light color, straight grain, fine, even texture, and is light in weight. It dries easily, is moderately stable in use, and, although not strong, is tough for its weight.

Black cottonwood has short, fine fibers and is used to produce pulp for high-grade book and magazine papers. The species peels easily, and its veneer is used as core and cross-banding stock in plywood and in baskets and crates. The light weight, good nailing characteristics, and light color of the lumber are ideal for manufacture of pallets, boxes, and crates. The lumber is also used in concealed parts of furniture. Fiberboard and flakeboard are made from black cottonwood. In early days, it was used for cooperage.

Genetics

Population Differences

Black cottonwood exhibits considerable variation throughout its range. Photoperiodic studies conducted under uniform environmental conditions in Massachusetts have shown that northern provenances cease growth earlier than southern provenances *(21)*. Moreover, cessation of growth among clones from the same latitude was related to length of the growing season (frost-free days) at places of origin (that is, elevation). Another study *(18)* conducted with clones indicates that several aspects of shoot growth are under genetic control: date of flushing, amount of early growth, growth rate in midseason, date of cessation, and average length of internode. A more recent study *(36)* demonstrated a large range of variation in leaf, branch, and phenology characters in 50 clones (five each from 10 natural populations growing in drainages west of the Cascade Range). Population means for several characters varied clinally with source latitude, longitude, and/or elevation. In general, southwestern clones developed smaller leaves, had more numerous and more erect branches, and continued growth later in the fall than northeastern clones. Experiments in pots and flats have shown that some clones of black cottonwood grow taller in the presence of another clone than when planted by themselves *(32)*.

Hybrids

Black cottonwood hybridizes freely with balsam poplar *(Populus balsamifera)* where the ranges of the two species overlap *(35)*. Another natural hybrid, the Parry cottonwood, resulting from crosses with *P. fremontii* is native to California. A hybrid *(Populus* × *generosa* Henry) between *P. angulata* (now considered either a variety or cultivar of *P. deltoides)* and *P. trichocarpa* was developed in England *(24)*. Also, *P. maximowiczii* × *trichocarpa* and *P. deltoides* × *P. trichocarpa* hybrids have been planted in the northeastern United States. Recent work in which *P. trichocarpa* was crossed with superior selections of *P. deltoides* from the southern United States has produced hybrids of markedly superior growth performance *(12,31)*.

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Populus L. Poplar Hybrids

Salicaceae Willow family

Maurice E. Demeritt, Jr.

Poplar hybrids (*Populus* spp.) are the result of natural and manmade crosses among poplar species. The genus is further divided into five sections of which four are represented in North America: *Leuce* (aspen type), to which *P. grandidentata* and *P. tremuloides* (bigtooth aspen and quaking aspen) belong; *Aigeiros* (cottonwood or poplar type), to which *P. deltoides, P. sargentii, P. fremontii*, and *P. wislizeni* (eastern, plains, Fremont, and Rio Grande cottonwood) belong; *Tacamahaca* (balsam poplar type), to which *P. balsamifera, P. trichocarpa*, and *P. angustifolia* (balsam poplar, black, and narrowleaf cottonwood) belong, and *Leucoides* (swamp poplar type), to which *P. heterophylla* belongs. *P. balsamifera* subsp. *trichocarpa* has been reported as the correct status of *P. trichocarpa (44)*.

Habitat

Native Range

Poplar hybrids occur naturally throughout the U.S. and Canada wherever compatible species come into close proximity (table 1). Most poplar hybrids, however, result from artificial hybridization and subsequent planting. The first large-scale hybridization project with poplars in the United States was begun in 1925 *(41,42)*. An unknown number of hybrids also form between native species and introduced clones, cultivars, and species. The Jackii poplar is a natural hybrid between *P. balsamifera* females and *P. deltoides* males. *Populus* × *Smithii* is a natural hybrid between *P. tremuloides* and *P. grandidentata*. Hybridization between *P. balsamifera* and *P. trichocarpa* occurs in the interior of southeastern Alaska and in the Cook Inlet region. Also, the trihybrid among *P. deltoides, P. balsamifera*, and *P. angustifolia* has been reported in southern Alberta.

Climate

In general, poplar hybrids grow best on humid and microthermal areas with adequate moisture during all seasons of the year. They are rarely found on sites that have temperatures of -46° C (-50° F) or on sites that have summer temperatures over 38° C (100° F) for more than a week.

Soils and Topography

Poplar hybrids grow best where soils are at least 1 m (3.3 ft) in depth to interrupted bedrock. The water table and porous or gravel layers should also be at least 1 m (3.3 ft) below the soil surface. Optimum pH ranges from 6.0 to 7.0, though some hybrids tolerate high or low pH conditions. Hybrids grow well on upland and bottom-land soils if the soils have good moisture-holding capacities and are of medium texture. Hybrids show extreme variation in tolerance of adverse site conditions. They grow best on soils of the orders Entisols, Inceptisols, Mollisols, Spodosols, and Ultisols.

Associated Forest Cover

The two natural hybrids, *P.* × *smithii* and *P.* × *jackii*, are associated with the parental species in the same stand, and the parental species dominate in the stands. The majority of hybrid poplars are planted in pure stands and all competing vegetation is controlled the first few years after planting. Poplars are very intolerant of shade and herbicides and also when young cannot tolerate competition from grass, weeds, and shrubs in their immediate area.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Poplar hybrids are dioecious and first flower at about 8 years of age. The flowers are borne in catkins (or aments) in the spring before leafing. Male and female catkins, when fully developed, are 10 to 15 cm (3.9 to 5.9 in) long. In the female flower, the number of stigmas varies from two to four and are either cap- or y-shaped. In the male flower, the number of stamens varies from 30 to 80. The bract has 20 to 30 digits, depending on the cultivar. The central areas of the bracts are light in color and the digits are dark brown, sometimes tinged with black *(34)*. Many poplar hybrids have never produced flowers and thus are thought to be sterile. Poplars flower between February and May and disperse seed between April and June of the same year. Intersection *Leuce* hybrids disperse seed a few weeks before intrasection *Aigeiros* and *Tacamahaca* or intersection *Aigeiros-Tacamahaca* hybrids. Fruits are one-celled capsules borne in long pendulous clusters (catkins), and each capsule is surrounded by tufts of

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Table 1—Naturally occuring hybrids among native populus species *(5,9,35)*

Parentage	Hybrid designation	Common name
P. alba × *P. grandidentata*	*P.* × *roulwauiana* Boivin	
P. alba × *P. tremula*	*P.* × *canescens* Sm.	
P. alba × *P. tremuloides*	*P.* × *heimburgeri* Boivir	
P. angustifolia × *P. deltoides*	*P.* × *acuminata* Rydb. (*P.* × *andrewsii* Sarg.)	Lanceleaf Cottonwood
P. angustifolia × *P. tremuloides*	*P.* × *sennii* Boivin	
P. balsamifera × *P. deltoides*	*P.* × *jackii* Sarg.	Jackii poplars
P. balsamifera × *P. tremuloides*	*P.* × *dutillyi* Lepage	
P. deltoides × *P. nigra*	*P.* × *euramericana* (Dode) Guinier (*P.* × *canadensis* Moench)	Euramerican poplars
P. deltoides × *P. tremuloides*	*P.* × *bernardii* Boivin	Bernard poplars
P. deltoides × *P. trichocarpa* (and reciprocal)	*P.* × *generosa* Henry (*P.* × *interamericana* Brockh.)	Interamerican poplars
P. fremontii × *P. trichocarpa*	*P.* × *parryi* Sarg.	Parry cottonwood
P. grandidentata × *P. tremuloides*	*P.* × *smithii* Boivin	
P. laurifolia × *P. nigra*	*P.* × *berolinensis* Dippel (*P. rasumowskyana* Schr. and *P.* × *petrowskyana* Schr.)	Berlin or Russian poplars
P. deltoides × *P. balsamifera* × *P. angustifolia* (natural trihybrid)	Unnamed	Unnamed

long, white, silky hairs attached to the short stalks of the seeds, promoting wind dispersion over great distances *(36)*.

Seed Production and Dissemination—Poplar hybrids generally are prolific annual seed producers. Individual trees of *Populus tremula*, an exotic, may yield from 8,000 to 54,000,000 seeds per year; hybrid poplar seed yields are thought to be the same. In *Populus deltoides* var. *virginiana* 35 liters (1 bushel) of fresh fruit yields about 0.9 kg (2 lb) of seeds. *Populus* seeds range in weight from 310,900 to 16,650,000 seeds/kg (141,000 to 7,550,000 seeds/lb) depending on the species, location, and tree *(36)*. The seeds are disseminated some distance from the mother tree by the wind. Natural seed dispersal begins at the same time as seed dispersal of the associated pure species in the area. In northern New England, hybrids of inter- and intrasectional crosses involving *Aigeiros* and *Tacamahaca* sections disperse seeds about June 1. Hybrids growing south of northern New England disperse seeds somewhat earlier.

Seedling Development—Germination is epigeal. Seedlings develop best on moist mineral soils where competing vegetation is minimal for 1 or 2 years after establishment. Seed germination capacity is retained only a few days under natural conditions. Seeds of *Populus deltoides* can be stored for at least 6 years at -20° C (-4° F) and 6 to 10 percent moisture without substantial loss in viability *(43)*.

Vegetative Reproduction—Poplar hybrids reproduce vegetatively by natural and artificial means. *Leuce*-type hybrids root best from root sections, though some selections root adequately from dormant stem cuttings. *Aigeiros*-type hybrids reproduce well from either greenwood or dormant stem cuttings, although most hybrids are reproduced from dormant cuttings. Dormant cuttings are produced predominately from hybrid stool beds established for that purpose. The cuttings are usually harvested in January to February, and stored in a cold chamber, or frozen as whips or cuttings, until planting. The whips or cuttings should not be allowed to desiccate. Cuttings should be soaked in water for at least 24 hours before planting. When hybrid poplars are planted in open fields or in areas with competing vegetation, good control of weeds, grasses, and vegetation is necessary for the poplars to survive. To establish poplar plantings by vegetative means the following steps should be taken: 1) plow or rototill the area during the summer before planting; 2) disk, cultivate, or rototill the area several times during the summer and fall so weeds, grass, and vegetation will not gain a foothold; 3) disk, cultivate, or rototill in the spring before planting; 4) plant the poplars at the desired spacing; 5) cultivate frequently the first 2 years to eliminate competition. As early as 1945, it was established that hybrid poplars performed best in a sod- and weed-free field *(37)*. More recent studies have shown cultivation to be advantageous *(4,15,16,17,45)*. If step 5 is omitted, heavy sod and weed cover will reduce tree survival and growth.

Weed control can be accomplished by use of chemicals, but these can be very injurious to hybrid poplars. Chemicals are not recommended unless great care is taken in their handling and use.

Sapling and Pole Stages to Maturity

Growth and Yield—Poplars grow best on fertile soils, and early height growth can average 1.2 to 1.8 m (4 to 6 ft) per year *(7,8)*.

Superior clones of poplar hybrids established with dormant cuttings spaced 1.2 by 1.2 m (4 by 4 ft) on two upland sites in Williamsburg, MA (fig. 1) produced 2.5 to 15.3 m^3 (1 to 6 cords) at 4 years, 7.6 to 35.7 m^3 (3 to 14 cords) at 9 years, and 56.1 to 117.2 m^3 (22 to 46 cords) at 15 years *(38)*. Poplar hybrids growing on a reclaimed strip-mine site in Pennsylvania have maintained an average growth of 1.2 m (4 ft) per year and have reached 19.8 m (65 ft) in height growth after 16 growing seasons, producing an average of 12.6 m^3/ha (2 cords/acre) per year *(6)*. Early field tests of closely spaced *Populus* 'Tristis' hybrids at 4 years of age produced 11.2, 12.6, and 7.6 t/ha (5.0, 5.6, and 3.4 dry tons/acre) per year of stems and branches at spacings of 0.23 m (0.75 ft), 0.30 m (1 ft), and 0.61 m (2 ft), respectively *(12)*.

Rooting Habit—*Aigeiros*-type hybrids have strong horizontal surface roots from which plunging roots develop. *Leuce*-type hybrids develop plunging roots constituting 40 to 50 percent of their entire root system. In other poplar hybrids, horizontal roots have been measured at 15 m (50 ft) for a 10-year-old tree growing in sandy soil, 20 m (66 ft) for an old tree, and 18 m (60 ft) for an old *Populus alba*. The development of plunging roots is limited by the level of the water table or by the soil condition *(1)*.

Reaction to Competition—Poplars and poplar hybrids are very intolerant of shade in the forest community, especially in comparison with other more shade- and competition-tolerant species. Poplar hybrids are usually established in pure plantings, using dormant cuttings. With this method, hybrids cannot tolerate weed, grass, and shrub competition during the first 2 years after planting. Space around each tree is also needed during the growth of the stand. If branches of trees overlap, growth and vigor are reduced and recovery of growth rate is slow.

Damaging Agents—In the Northeast, poplar hybrids are susceptible to many diseases and insects. Disease organisms that cause stem canker are hypoxylon canker *(Hypoxylon mammatum)* that infects aspens and their hybrids in low stocked stands; cytospera canker *(Cytospera chrysosperma)* that infects poplar hybrids and is promoted by moisture stress; dothichiza canker *(Dothichiza populae)* that causes decline in Lombardy poplar; septoria leaf spot *(Septoria musiva)* that causes severe stem infections in densely stocked stands; and pecan feeder root necrosis *(Fusarium solani)* that may develop in stems under 2 years old.

Foliage diseases of varying severity are melampsora leaf rust *(Melampsora medusae)*, marssonina leaf spot *(Marssonina brunnea)*, oak leaf fungus *(Septotinia podophyllina)*, shepherd's crook shoot blight *(Venturia populina)* on *Tacamahaca* poplars, *V. macularis* on *Leuce* and *Aigeiros* poplars), and a leaf spot *(Phyllosticta* spp.).

The most serious defoliator of poplar hybrids, especially young trees, is the cottonwood leaf beetle

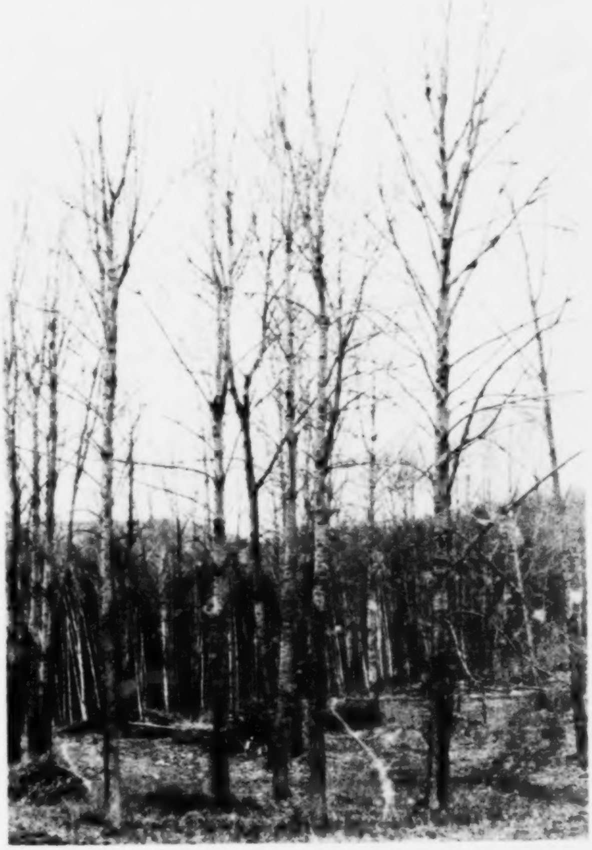

Figure 1—*Hybrid poplar clonal test planted in 1952 at Williamsburg, MA.*

(Crysomela scripta). The forest tent caterpillar *(Malacosoma disstria)*, the poplar tentmaker *(Ichthyura inclusa)*, the spiny elm caterpillar or mourning cloak butterfly *(Nymphalis antiopa)*, and the large aspen tortrix *(Choristoneura conflictana)* can also cause complete defoliation. Leaf damage may also be inflicted by a leaf beetle *(Zeugophora scutellaris)*, the aspen blotch miner *(Phyllonorycter tremuloidiella)*, and the aspen leafminer *(Phyllocnistis populiella)*.

One of the most destructive poplar pests is the cottonwood twig borer *(Gypsonoma haimbachiana)*. It kills buds and up to 25 cm (10 in) of shoot tips. Other borers that do damage are the poplar-and-willow-borer *(Cryptorhynchus lapathi)*, the poplar borer *(Saperda calcarata)*, the cottonwood borer *(Plectrodera scalator)*, the bronze poplar borer *(Agrilus liragus)*, and a flatheaded borer *(A. horni)*.

Infestations of the poplar gall midge *(Prodiplosis morrisi)* and various aphids and plant lice may reduce the growth of individual trees *(9)*.

Special Uses

Hybrid poplars were initially developed for conventional pulpwood *(42)*. In recent years, more interest has been placed on evaluation of hybrid poplar for short-rotation chip production for pulp and energy uses *(4,21,27,28,29)*. However, at this time, investment rates of return are not attractive for large scale conversions to short rotation intensive culture systems *(4,14)*.

There are many estimates of poplar hybrid biomass yields in the literature, but the following values are averages from intensively managed plantations on many sites in the northeastern United States *(9)*: First-year height growth is 0.9 to 2.4 m (3 to 8 ft); mean annual height growth after 10 to 20 years is 0.9 to 1.4 m (3 to 4.5 ft); mean annual diameter growth after 10 to 20 years is 1.0 to 1.5 cm (0.4 to 0.6 in); mean annual volume increment after 10 to 20 years is 7.0 to 24.5 m^3/ha (100 to 350 ft^3/acre); and mean annual biomass increment after 5 to 20 years is 4.5 to 20.2 t/ha (2 to 9 tons/acre).

Growth and yield vary appreciably depending on location, site quality, clone or cultivar used, and silvicultural conditions. These values given are only generally representative. Diameter growth of individual trees depends heavily on stocking density. Wide spacings or frequent thinnings promote rapid diameter growth.

Biomass consists of ovendry, leafless stems and branches. Attainment of maximum mean annual increment occurs only if stands are heavily fertilized and irrigated and occurs much sooner at tree spacings of 2 m (6.6 ft) or less.

In the northeastern United States, moose and deer often browse on poplar hybrids in recently planted plantations. Poplar buds are a choice food supply for ruffed grouse and several kinds of songbirds. Grouse and pheasant also eat the catkins.

In urban areas, poplar hybrids are useful where fast-growing trees are needed for shade, landscaping, and screening around industrial buildings, apartment complexes, recreational playing areas, parking lots, and landfills. These trees live less than 100 years so more tolerant species should be interplanted with them.

Poplar hybrids are used to stabilize soils on hillsides, along streams and rivers, landfills, and borrow pits. They are also planted as fence rows to reduce air speed in agricultural areas where soil is transported by the wind.

Hybrid poplars have been extensively used as test organism for research studies because of their ease of propagation, fast growth, and the variety of clonal parentages. They have been used to study the effect of air pollutants *(2,3,10,13,18,19,22,23,24,25,26,30,31,32,33,46)* and wood compartmentalization *(11,39,40)*, to name just two.

Genetics

Approximately 30 species of poplars are available for hybridization as listed below; however, not all possible crosses have been successful or seem feasible at this time (fig. 2).

Classification of Populus *(47)*

Section and Species	*Geographic distribution*
Turanga Bge.	
euphratica Olivier (syn: *pruinosa* Schrenk)	West and Central Asia, North Africa
Leuce Duby	
adenopoda Maxim.	China
alba L.	Europe, Asia, North Africa
davidiana (Dode) Schneid.	Northeast Asia
grandidentata Michx.	North America
sieboldii Miq.	Japan, Korea
tomentosa Carr.	Asia
tremula L.	Europe, Asia
tremuloides Michx.	North America
Leucoides Spach	
ciliata Wall	Central Asia
heterophylla L.	Southeastern United States
lasiocarpa Oliv.	China
wilsonii Schneid.	China
Tacamahaca Spach	
angustifolia James	North America
balsamifera L.	North America
cathayana Rehd.	Northeast Asia
koreana Rehd.	Korea
laurifolia Ledeb.	Siberia
maximowiczii Henry	Northeast Asia, Japan

simonii Carr.	Asia
suaveolens Fisch.	Asia
szechuanica Schneid.	China
trichocarpa Torr. & Gray	North America
yunnanensis Dode	China
Aigeiros Duby	
deltoides Bartr. ex Marsh.	North America
deltoides var. *occidentalis* Rydb. (syn: *sargentii* Dode)	North America
fremontii Wats.	North America
fremontii var. *wislizeni* Wats. (syn: *wislizeni* Wats.)	North America
nigra L.	Europe, Asia, North Africa

An example of the genetics of one cultivar follows. One of the widely grown hybrid cottonwood cultivars is 'Robusta,' reportedly *Populus angulata* × *P. plantierensis*. *Populus angulata* is a clone of eastern cottonwood (*P. deltoides* var. *deltoides*); *P. plantierensis* is a hybrid of a western European black poplar (*P. nigra*) and Lombardy poplar (*P. nigra* var. *italica*). Lombardy poplar is a fastigate form of black poplar, native to Iran. *Populus nigra* var. *betulifolia* of western Europe is distinguished from the more easterly forms by the slightly hairy petioles and tips of young shoots. These are found in *P. nigra* var. *plantierensis* and transferred to the 'Robusta' clones. Good apical dominance, numerous side branches, and very narrow branch angle are traits inherited as a single dominant gene. Lombardy poplar is homozygous with respect to this gene, while *P. nigra* var. *plantierensis* is heterozygous with respect to this gene (20).

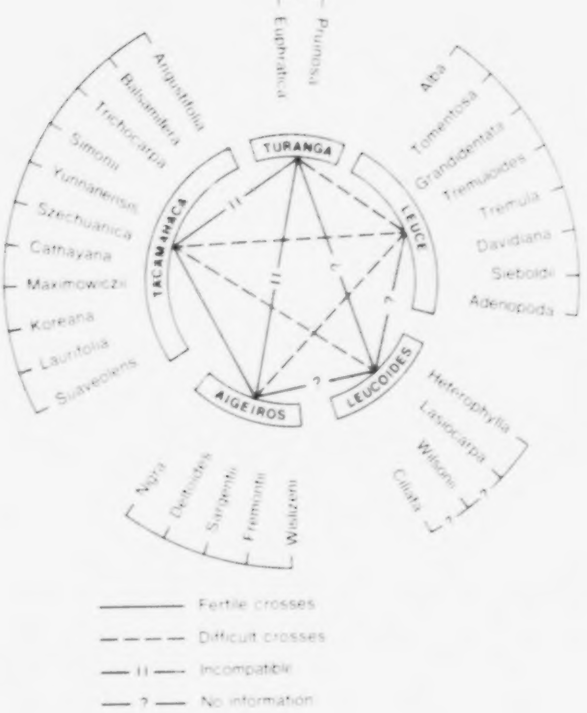
?
Euphratica
Pruinosa
TURANGA
Angustifolia
Balsamifera
Trichocarpa
Simonii
Yunnanensis
Szechuanica
Cathayana
Maximowiczii
Koreana
Laurifolia
Suaveolens
TACAMAHACA
Alba
Tomentosa
Grandidentata
Tremuloides
Tremula
Davidiana
Sieboldii
Adenopoda
LEUCE
AIGEIROS
Nigra
Deltoides
Sargentii
Fremontii
Wislizeni
LEUCOIDES
Heterophylla
Lasiocarpa
Wilsonii
Ciliata
?
Fertile crosses
Difficult crosses
Incompatible
No information

Figure 2—*Summary of interspecific breeding in the genus* Populus (7).

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Prosopis pallida (Humb. & Bonpl. ex Willd.) H.B.K. Kiawe

Leguminosae Legume family

Roger G. Skolmen

Kiawe (*Prosopis pallida*), also known as algarroba or bayahonda, is one of the 44 species of *Prosopis* recognized. The genus has a confused taxonomy. Burkart's revision, used here, assigns the designation *P. pallida* to the species introduced into Puerto Rico and elsewhere in the Caribbean formerly called *P. juliflora*. *Prosopis glandulosa*, mesquite, also formerly included in *P. juliflora* and four to six other species grow as shrubs or trees over an extensive area of the Southwestern United States and Northern Mexico *(2,7,10)*.

More than 60 700 ha (150,000 acres) of dry kiawe forests in Hawaii are descended from a single tree planted in 1828 at the corner of a church in Honolulu. That year, Father Bachelot, the first Catholic priest in the Hawaiian Islands, planted a tree that he had raised from a seed he had brought with him from Paris. The tree was later determined to be *Prosopis pallida*. In August 1832, the tree was found to be bearing fruit. By 1840, progeny of the tree had become the principal shade trees of Honolulu (fig. 1) and were already spreading to dry, leeward plains on all of the islands *(3,8,12)*.

Habitat

Native Range

Kiawe is native to the drier parts of Peru, Colombia, and Ecuador, especially near the coast. It is naturalized in Hawaii and Puerto Rico *(10)*.

Climate

In Hawaii, kiawe is most common in leeward coastal areas that have an annual rainfall of 250 to 760 mm (10 to 30 in) and a mean annual temperature of 24° C (75° F) with a range of 13° to 35° C (55° to 95° F). In a California study *(6)*, kiawe trees less than 3 years old survived –2° C (29° F), but were killed at –6.1° C (21° F). Kiawe rarely extends above 150 m (500 ft) in elevation because higher rainfall and lower temperature give other species competitive advantage. In a few locations, however, it reaches an elevation of about 610 m (2,000 ft). In its native habitat, it is reported to grow from sea level to 300 m (990 ft) in annual rainfall from 250 to 1240 mm (10 to 49 in) (11). On the Islands of Lanai, Kahoolawe, and Niihau, which are in the lee of larger islands, kiawe occupies both windward and leeward shores extensively. It is present also as a shrub on some windward coasts of all islands.

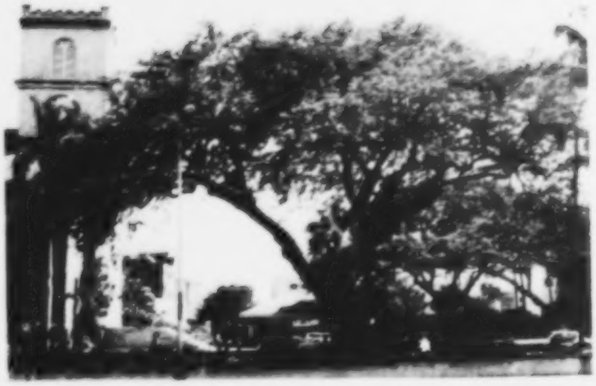

Figure 1—*A kiawe, already a large tree when first photographed in 1855, that continues to grow in the Kawaiahao Church yard, Honolulu.*

Many old kiawe trees have been saved as garden and park trees during land development and have grown to large sizes with irrigation. Although it is a coastal species, kiawe is defoliated by windblown salt spray of winter storms *(3)*.

Soils and Topography

Kiawe grows well on the soils that form on the arid or semiarid coastal lands of leeward Hawaii (fig. 2).

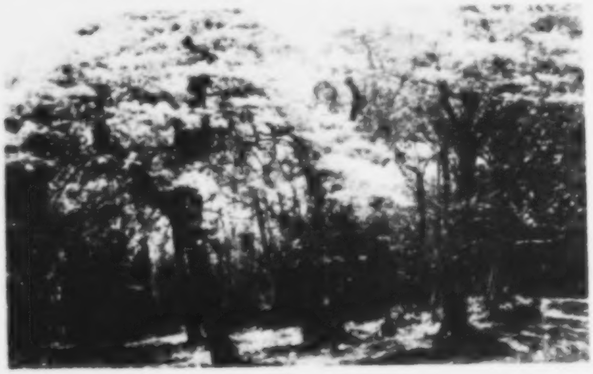

Figure 2—*Typical roadside kiawe trees near Honolulu.*

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It is also very tolerant of saline soils *(11)*. The soils where it grows in Hawaii are primarily Inceptisols, Mollisols, and Vertisols. The Inceptisols are in the great group Eutrandepts (reddish-brown latosols) developed from basaltic rock or ash. The Mollisols are Haplustolls (low humic latosols) developed from basaltic material and alluvium. The Vertisols are Chromusterts (dark magnesium clays) developed from alluvium and coral limestone and Torrerts developed from olivine basalt. These soils are mostly neutral to moderately alkaline in reaction, frequently stony to very stony, and occupy level to moderately steep coastal lands. In the driest locations, such as the eastern slopes of the Island of Lanai, kiawe is confined to the gully bottoms. Elsewhere, it extends onto ridges.

Associated Forest Cover

Kiawe is usually found in association with koa haole *(Leucaena leucocephala)*, opiuma *(Pithecellobium dulce)*, and klu *(Acacia farnesiana)*. It is sometimes associated with the native tree, wiliwili *(Erythrina sandwicensis)*, the native shrub, a'alii *(Dodonaea viscosa)*, and the introduced shrub, lantana *(Lantana camara)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—In Hawaii, kiawe begins to flower when 3 to 4 years old. The tree can flower at any time of the year and frequently flowers twice a year. Usually, it flowers from January to March, but in some years with wet summers it also flowers heavily during September and October. The numerous small perfect flowers are borne in pale yellow spikes 7 to 10 cm (3 to 4 in) long and about 13 mm (0.5 in) in diameter. Styles protrude from the corolla just before it opens, but when it is opened the style and the 10 stamens are about the same length. Flowers are insect pollinated. Kiawe is an excellent honey tree *(3)*.

About 6 months after flowering and pollination, the pods ripen and fall to the ground in April and July, or in normally dry years, only in July. The pods are straight or slightly curved yellowish beans 7 to 20 cm (3 to 8 in) long by 8 mm (0.3 in) wide; there are 350/kg (160/lb) *(18)*.

Seed Production and Dissemination—Pods do not open on drying to release their seed as some other legumes do. Instead, seeds are released either by natural decomposition of the pods or by passage of the seeds through the digestive system of an animal. From 10 to 20 light brown seeds per pod are encased in a sticky, sugary pulp. Seeds are difficult to extract from the pods. It is possible, however, to obtain seed by running pods through a commercial meat grinder with 1-cm (0.4-in) holes *(5)*. There are about 28,500 to 32,000 seeds per kilogram (13,000 to 14,500/lb). The seeds can be stored at ambient room temperature, protected from insects, for 9 months with little loss of viability *(18)*. Germination is improved slightly by scarifying the seeds with hot water before sowing. Scarification with concentrated sulfuric acid for 10 minutes improved germination from 64 percent (without treatment) to 88 percent *(18)*.

Many seeds are destroyed by insect pests. In Hawaii, a black beetle, *Mimosestes amicus*, bores into the pods that have fallen to the ground *(16)*. In Puerto Rico, a Bruchid weevil attacks seed on the tree, causing seed from green pods on the tree to have a germination rate of only 59 percent, yellow pods on the tree only 40 percent, and pods on the ground only 6 percent *(18)*.

Seedling Development—Germination is epigeal. Seedlings are usually found associated with animal droppings during and after rainy periods. In this highly fertile situation, seedlings grow rapidly, reaching 0.3 m (1 ft) in 3 to 4 months. Even in the absence of browsing animals, kiawe reproduces prolifically on abandoned city house lots containing older trees. Seedlings in such a situation can grow more than 1 m (3 ft) tall in the first year if rainfall is adequate. Seedling survival depends primarily on sufficient rainfall during 4 to 6 weeks after germination. The seedlings are also intolerant of shade.

Vegetative Reproduction—Kiawe stumps often sprout after being cut. Some thornless trees have been propagated by air-layering of the mature branches, but only on an experimental scale. Kiawe cuttings can also be rooted under mist *(5)*.

Sapling and Pole Stages to Maturity

Growth and Yield—The oldest kiawe trees in Hawaii of known age are at the entrance to Punahou School in Honolulu. This area was a treeless field in 1848. In 1918, trees on this site that were about 70 years old ranged from 61 to 104 cm (24 to 41 in) in d.b.h. and from 20 to 26 m (65 to 85 ft) in total height *(9)*. This is a relatively wet area for kiawe, with an annual rainfall of 940 mm (37 in) and abundant groundwater from a nearby spring.

At Waianae, Oahu, an area with 510 mm (20 in) annual rainfall, a tract of kiawe trees of unknown age yielded 226.8 m^3 per ha (3,240 ft^3/acre or 36 cords/acre). On Maui, a 2.4-ha (6-acre) area with 380 mm (15 in) rainfall yielded 365.4 m^3 per ha (5,220 ft^3/acre or 58 cords/acre) *(9)*.

In Puerto Rico, on a dry, gravelly site (760 mm or 30 in rainfall), a 21-year-old planting had trees 25 to 36 cm (10 to 14 in) d.b.h. and 4.6 to 7.6 m (15 to 25 ft) tall *(18)*.

In Honolulu, the original tree, when measured in 1916, at 88 years of age, was 99 cm (39 in) in diameter *(8)*. But the champion kiawe tree in Hawaii is at Puako, Island of Hawaii, and measures 130 cm (51 in) d.b.h. and 27.7 m (91 ft) tall *(1)*.

In a study of biomass production of other *Prosopis* spp. in southern California *(5)*, several species, mostly from South America, were grown for 3 years at 1.2 m (4 ft) spacing and three levels of irrigation. These trees produced an annual average of 8.5 t/ha (3.8 tons/acre) of fresh biomass. Another study in Texas *(19)* determined that *Prosopis* natural stands yielded 19.3 t/ha (8.6 tons/acre) on deep upland soils and 36.1 t/ha (16.1 tons/acre) on deep bottom land.

In Puerto Rico, direct seeding in dry areas (760 mm or 30 in rainfall) gave poor survival, but planting of seedlings produced 67 percent survival despite a severe 6-month drought *(18)*.

On windy or dry sites, kiawe grows as a shrub, or a small twisted tree only 3 to 5 m (10 to 16 ft) tall. It is usually layered where it grows in strong trade winds and lies along the slopes as a rounded bush.

Rooting Habit—The genus *Prosopis* is noted for its ability to root deeply *(10)*. A *Prosopis velutina* tree in Arizona was found with roots extending downwards 53 m (174 ft) into the ground *(10)*. Kiawe seedlings produce strong, rapidly growing taproots that appear to be capable of deep extension and may share the deep rooting characteristic common to the genus. The species can grow on windy, dry sites, which suggests that its roots penetrate deeply to reach moisture. Trees on such sites are small. Trees on coastal plains where abundant, shallow groundwater is available reach large size, but are shallow-rooted and subject to windthrow *(3,9)*.

Reaction to Competition—Kiawe is an intolerant tree and is shaded out by faster growing plants on wet sites. On dry sites the grasses, koa haole, and opuima, with which it commonly associates, remain so sparse that abundant sunlight reaches the kiawe.

No silviculture is practiced with kiawe, but the species' characteristics indicate that it could be managed as a fuelwood crop. It fixes nitrogen, so requires less fertilizer than nonleguminous trees, and it coppices after cutting, so does not require replanting at each rotation. It is a short-boled, crooked tree even when grown at close spacing and appears unsuitable for use as a timber tree.

Damaging Agents—Kiawe trees are severely defoliated by the introduced caterpillar *Melipotis indomita* but quickly leaf out again after defoliation *(17)*. They are also sometimes partially defoliated by the Blackburn butterfly, *Vaga blackburni*, an insect that usually does more damage to other legumes *(16)*. In California, a psyllid, *Alphalaroida* spp., caused leafroll of new leaflets in plants grown in a glasshouse *(6)*. The kiawe roundheaded borer, *Placosternus crinicornis*, infects trees under stress, and recently cut firewood, boring under the bark and into the sapwood *(18)*. Carpenter bees seem to have a particular affinity for the sapwood of kiawe fence posts.

The tree grows in areas where fire hazard is often extreme. It is usually killed outright by fire and burned trees almost never sprout.

Special Uses

Kiawe is used principally as a cover tree for erosion control on arid land. As recently as 1915, it was considered the most valuable tree in Hawaii for a variety of other reasons. Its pods and seed are nutritious fodder. The pods alone contain 9 percent protein and the seeds 34 percent, one of the highest levels for any legume. But because the seed coats are indigestible, the seeds must be ground, if animals are to recover this protein. In 1935, Hawaii shipped more than 200 tons of kiawe honey. A small honey industry in Hawaii continues to depend on kiawe *(3,6,9)*.

The wood is extremely hard and heavy. It is used directly for fuel and also is made into charcoal. The heartwood is durable and kiawe is preferred for fence posts despite its crooked form. Mesquite, a related species in the United States, is the traditional wood used for boatbuilders' calking mallets and, in Hawaii, kiawe is preferred for cement floats.

Genetics

Because the entire population of kiawe in Hawaii is originally from one tree, inbreeding has been intensive. One possible recessive characteristic of the population is thornlessness. Although most kiawe trees have thorns with strong spines often 2.5 cm (1 in) long, an estimated 25 percent of the mature trees produce only small, hard stipules rather than long, spikelike spines at the twig nodes. The thornless characteristic has been noted for years, and as early as 1937, Hawaii shipped seed from thornless kiawe trees to Cuba, Arabia, Australia, Fiji, and South Africa *(3)*. Attempts have been made to breed for thornlessness, but have so far been unsuccessful. Thornless trees can be propagated by air-layering of mature twigs *(13)*. Some other *Prosopis* spp. also exhibit thornlessness among individuals in the populations *(10)*. Thornlessness can be seen in some or all of these other species when they are only 3 to 4 months old *(4)*.

One report states that *Prosopis* spp. bear self-incompatible flowers *(15)*. This is obviously not true of *Prosopis pallida*, or at least of that one individual *Prosopis pallida* originally introduced into Hawaii.

Another report mentions that in 1920, the U.S. Department of Agriculture's Experiment Station in Honolulu had imported seed and was growing seedlings of a number of other *Prosopis* spp. in an attempt to determine the identity of the tree common to Hawaii by comparison *(14)*. No record exists of the disposition of these seedlings, but a possibility exists that they may have been outplanted. No hybrids are known in Hawaii, however.

In addition to kiawe, at least five other *Prosopis* species deserve consideration for use in arid lands for firewood, forage, and cover *(10)*. One of these, *Prosopis alba*, is the backbone of the Arizona nursery shade tree industry *(4)*.

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Prunus pensylvanica L. f. Pin Cherry

Rosaceae Rose family

G. W. Wendel

Pin cherry *(Prunus pensylvanica)* is a small common tree inhabiting a great variety of lands in the northern part of the United States and Canada. It is sometimes called fire cherry for its value as a reforesting agent after forest fires. It forms pure stands that provide shade for seedlings of slower growing species, then dies off, making way for the new trees. Another common name, bird cherry, reflects the prevalent use of the fruit by birds as food. It is also called northern pin cherry, wild red cherry, and pigeon cherry. The soft porous wood is of little commercial value.

Habitat

Native Range

Pin cherry (fig. 1) grows from Newfoundland and Labrador west to southern Mackenzie District and British Columbia in Canada. Scattered stands are found south in the Rocky Mountains to Montana and Colorado; southeastward from the Black Hills of South Dakota to Iowa, Illinois, Pennsylvania, and New Jersey, northeast to New England. In the Southeast its range follows the Appalachian Mountains south to northern Georgia and eastern Tennessee.

Climate

Throughout the range of pin cherry, the mean annual number of days with minimum temperatures below 0° C (32° F) is 90 in the southern Appalachians to more than 180 in the northern and western part of the range *(28)*. Normal annual total precipitation ranges from 2030 mm (80 in) in the Great Smoky Mountains to 410 mm (16 in) in the western part of the range. Mean annual total snowfall ranges from 61 cm (24 in) in the southern Appalachians to 254 cm (100 in) in the northern part of the range. Normal daily temperatures vary widely throughout the range of pin cherry:

	Southeast		Northeast and West	
	C	*F*	*C*	*F*
January max.	10°	50°	–1°	30°
July max.	27°	80°	29°	85°
January min.	–4°	25°	–23°	–10°
July min.	16°	60°	4°	40°

Soils and Topography

Pin cherry grows on infertile rocky ledges, sandy plains, moist loamy soils, and rich loams *(14)*. Throughout the Appalachian Mountains, the soils fall into the general order of Inceptisols. In New England and eastern Canada, Spodosols predominate. Around the Great Lakes, Alfisols are the major order with some Histosols and Spodosols. In the Rocky Mountains of the United States and Canada pin cherry grows on soils belonging to the general orders of Alfisols, Entisols, and Mollisols.

On bituminous coal banks in central Pennsylvania, pin cherry and trembling aspen are the most abundant pioneer tree species and may account for 33 percent of the plant cover in 10 years *(6)*. Pin cherry usually follows the distribution of Kellogg's great soil groups — Podzol, Gray-Brown Podzolic, and Lithosol *(19)*.

In the White Mountains of New Hampshire, pin cherry is a major component in rock and soil slide successions but is usually far more numerous after wind-throw, logging, or light fires because its presence depends on seed buried in the forest floor *(11)*. In the aspen communities of the Lake States, pin cherry is abundant on the moist and clayey soils *(7)*.

Pin cherry, though mainly a northern species, regenerates naturally throughout most of its range after a heavy cutting or fire. In the central and southern Appalachian Mountains, it is most common at elevations above 915 m (3,000 ft). On the "heath" balds at higher elevations in the southern Appalachians, pin cherry may be a major component. In New England, pin cherry stands are underlain by a wide range of soils including unstratified glacial till derived from acidic and relatively infertile parent materials. The soils are shallow, well-drained Spodosols and range from very stony to extremely stony sandy loams to loams.

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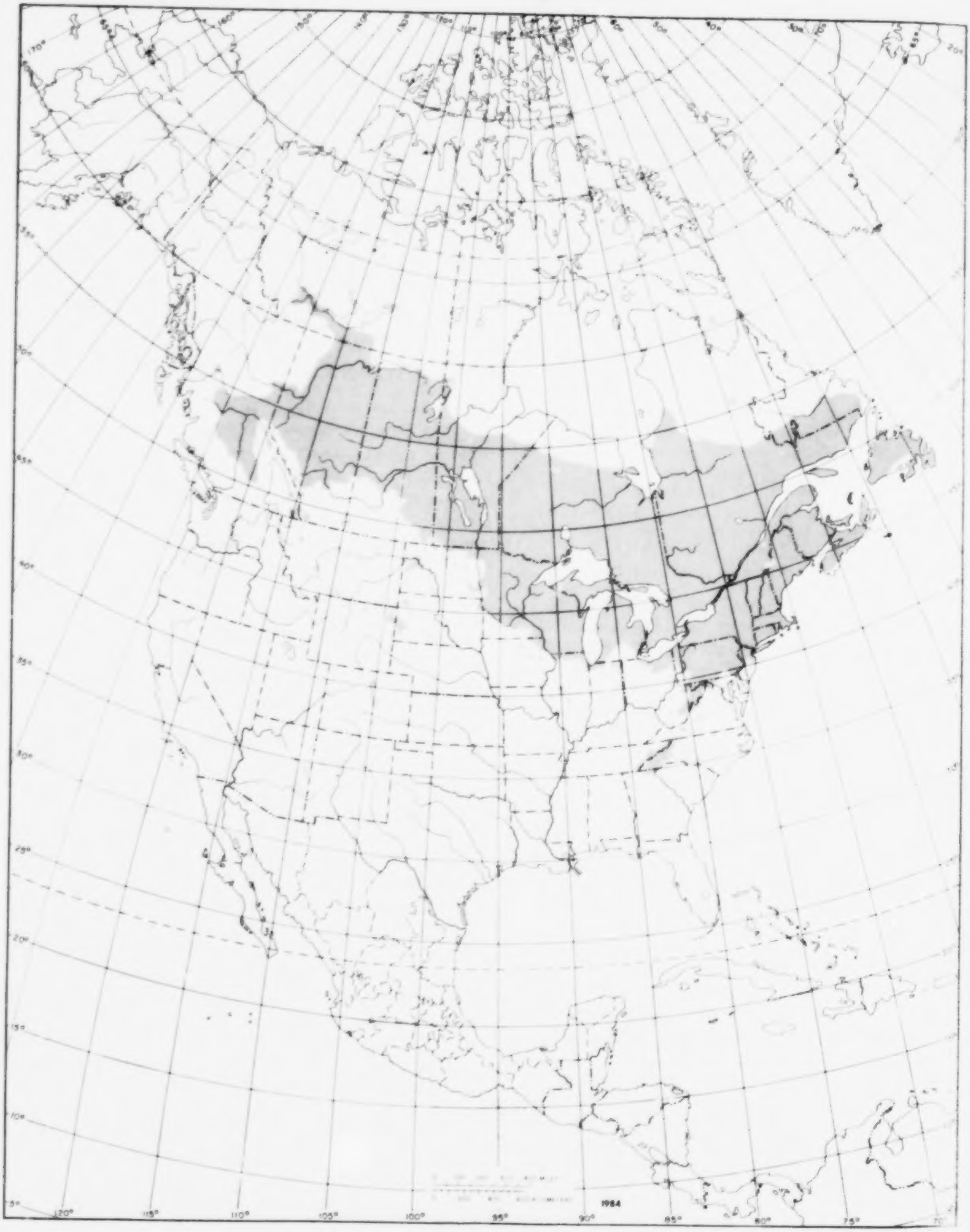
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Figure 1—*The native range of pin cherry.*

Associated Forest Cover

Pin cherry, in pure stands or as a majority of the stocking, is the forest cover type Pin Cherry (Society of American Foresters Type 17) *(14)*. It is frequently associated with quaking aspen and bigtooth aspen *(Populus tremuloides* and *P. grandidentata)* paper birch and yellow birch *(Betula papyrifera* and *B. alleghaniensis)*, striped maple, red maple, and sugar maple *(Acer pensylvanicum, A. rubrum*, and *A. saccharum)*, American beech *(Fagus grandifolia)*, northern red oak *(Quercus rubra)*, balsam fir *(Abies balsamea)*, and red spruce *(Picea rubens)*. Fraser fir *(Abies fraseri)* and American mountain-ash *(Sorbus americana)* are additional associates in the southern Appalachians. Chokecherry and black cherry *(Prunus virginiana* and *P. serotina)* are common associates in the Lake States.

Pin cherry is a component of the following forest cover types:

16	Aspen
17	Pin Cherry
18	Paper Birch
19	Gray Birch–Red Maple
20	White Pine–Northern Red Oak–Red Maple
21	Eastern White Pine
25	Sugar Maple–Beech–Yellow Birch
28	Black Cherry–Maple
32	Red Spruce
34	Red Spruce–Fraser Fir
60	Beech–Sugar Maple
108	Red Maple

In addition to the understory tree species in pin cherry stands, numerous shrubs and forbs occur, including blackberry *(Rubus* spp.), redberry elder *(Sambucus pubens)*, hobblebush *(Viburnum alnifolium)*, American yew *(Taxus canadensis)*, dwarf raspberry *(Rubus pubescens)*, wild sarsaparilla *(Aralia nudicaulis)*, largeleaf aster *(Aster macrophyllus)*, mountain aster *(A. acuminatus)*, violets *(Viola* spp.), bracken *(Pteridium aquilinum)*, spinulose woodfern *(Dryopteris spinulosa)*, and shining clubmoss *(Lycopodium lucidulum) (14)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pin cherry flowers from late March to early July. Flower buds are formed in August or September of the preceding year *(17)*. In Warren County, PA, flowers appear from May 1 to May 15. The perfect flowers are white and 12 to 16 mm (0.47 to 0.63 in) broad with long pedicels; they are borne in corymbs or umbels and expand with the leaves. The globose fruits ripen from July to September, depending on locality. They are light red, 5 to 7 mm (0.20 to 0.28 in) in diameter, and have thin, acid flesh and subglobose stones 4 to 5 mm (0.16 to 0.20 in) long *(9,10,16)*. Fruiting occurs as early as age 2 in natural stands in Pennsylvania *(16)*. Sexual maturity of natural dominant trees in New Hampshire may be attained during the fourth growing season though large quantities of fruits are not produced until several years later *(23)*.

Seed Production and Dissemination—Fruits are dispersed by gravity and to a much lesser degree by birds and small mammals after the fruits ripen in July *(12)*. The weight of cleaned seeds per 45 kg (100 lb) of fruit ranges from 7 to 12 kg (16 to 27 lb). The number of cleaned seeds per kilogram ranges from 17,600 (8,000/lb) to 48,100 (21,800/lb) and averages about 31,300/kg (14,200/lb) *(16)*.

In a 4-year study on the Monongahela National Forest in West Virginia, trees with an average d.b.h. of 12 cm (4.7 in) yielded 0.64 liter (0.68 qt) of fruit per tree *(26)*. Half the trees bore fruit, and fruit yields varied substantially from year to year. Fruits were produced at 3- to 4-year intervals. In New Hampshire, dominant trees produced some fruit at 4 years, but quantity production occurred later.

Despite its short life span of about 30 years, fruit production in pin cherry is high. For 15-year-old, open-grown trees in pure stands, annual fruit production was estimated at 2,762,500 fruits per hectare (1,118,000/acre). For 25-year-old pin cherry stands in the same area of New Hampshire, annual seed production was 2,324,500/ha (940,700/acre) *(23)*.

Many seeds remain buried in the soil in areas where pin cherry once grew. Some seeds are disseminated by birds that excrete or regurgitate the seeds at a distance from their source, and some are moved by mammals *(1,23)*. In two areas in New Hampsire, the average number of viable pin cherry seeds in the forest floor ranged from 345,000/ha (139,676/acre) to 494,000/ha (200,000/acre) *(23)*. In other New Hampshire stands, depending on stand age, the number of viable seeds in the forest floor ranged from 10,000 to 1,110,500/ha (4,050 to 450,000/acre) *(15)*. It has been estimated that some seeds buried in the soil retain their viability for 50 to 150 years *(15,22)*.

Seedling Development—Pin cherry germination is epigeal and most pin cherry reproduction arises from seed stored in the forest floor. In natural stands in northwestern Pennsylvania, Marquis *(24)* reported 36,800/ha (14,900/acre), 14,100/ha (5,700/acre), and

46,700/ha (18,900/acre) pin cherry seedlings germinating after removal of one-half, two-thirds, and all of the overstory, respectively.

In New England, more pin cherry seedlings germinated from soil blocks taken from 38- and 95-year-old stands than from 5- or 200-year-old stands *(15)*. More than 70 percent germinated during the first summer in the 38- and 95-year-old stand samples. The number of germinating seeds was 2, 111, 52, and 1 per m² (from fewer than 1 to 10/ft²) for the 5-, 38-, 95-, and 200-year-old stands, respectively.

In the central Appalachians in West Virginia, dense thickets of pin cherry frequently develop after clearcutting 40- to 70-year-old hardwood stands. On two areas 5 years after clearcutting, there were between 2,470 and 7,410 pin cherry seedlings/ha (1,000 and 3,000/acre) 0.3 m (1.0 ft) high and up to 2.5 cm (1.0 in) in d.b.h. and between 680 and 990 stems/ha (275 to 400/acre) 2.5 to 12.7 cm (1.0 to 5.0 in) d.b.h. *(25)*.

A small amount of pin cherry seed probably germinates annually in northern hardwood stands. However, seedlings have been reported to survive only in large openings where light and moisture were more available. The largest number of pin cherry seedlings appeared in response to major disturbances such as heavy cutting or burning *(23)*. In one study, mechanical removal of the endocarp and a cool temperature, 15° C (59° F), promoted better pin cherry germination. The germination rate of pin cherry was greatly improved by soaking seed for 24 hours in a chemical solution (0.5 M hydroxylammonium chloride) followed by a series of drastic temperature fluctuation treatments *(20)*. With this treatment the seed germination rate was more than 75 percent. Often pin cherry seed germination is less than 10 percent when seed viability is 100 percent. It appears that the factor triggering increased germination of buried pin cherry seed following forest disturbance is the more extreme temperature fluctuation created by removing the overstory *(20)*. Although the factors accounting for the natural germination of pin cherry could not be determined exactly, apparently (a) time is needed to age the endocarp so it becomes more permeable to water and oxygen, and (b) changes in soil and water chemistry in response to the altered microclimate of a disturbed site or to other conditions is necessary *(22)*.

In northeastern Pennsylvania, pin cherry germination generally increased with light under no moisture stress, but under normal moisture stress, germination was best under partial shade. Under heavy shade, pin cherry seedling mortality is high, but with increasing light, survival is increased. Growth of seedlings is rapid and directly related to the amount of light received *(24)*. Repeated applications of N to existing sawtimber stands could reduce the pin cherry component in future stands. In situations where pin cherry outgrows other more desirable species after regeneration cuttings, N fertilization might benefit maturing stands by increasing growth rates of residual trees and reducing the number of pin cherry seeds that would germinate and later compete with preferred reproduction *(2)*.

Ripened fruits of pin cherry should be collected from trees or from the ground in late summer. For storage the pulp should be removed and the seeds stored in sealed containers at 1° to 3° C (34° to 38° F). Seed viability has been retained for up to 10 years under these conditions *(12)*.

For nursery sowing, pin cherry seed should be stratified in moist sand for 60 days at alternating temperatures of 20° to 30° C (68° to 86° F) and for 90 days between 3° to 5° C (37° to 41° F) *(18)*.

Vegetative Reproduction—Because pin cherry suckers readily, it should grow well from root cuttings. Sour cherry is often grafted on pin cherry root stocks, but budding is a more common practice *(3,29)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Information on the growth and yield of pin cherry is scarce. In thickets, it forms a closed canopy in 3 to 7 years and reaches maturity in 20 to 40 years *(14)*. On dry, compact glacial till soils in New Hampshire, where pin cherry may comprise 50 percent of the species composition in sapling stands, mean annual biomass production was 3290 kg/ha (2,931 lb/acre), mean annual basal area growth was 1.30 m²/ha (5.66 ft²/acre), mean annual d.b.h. growth was 2 mm (0.08 in), and mean annual height growth was 0.23 m (0.75 ft) *(21)*.

When young stands of northern hardwoods are cut, nearly pure stands of pin cherry often become established. When the pin cherry dies, the succession is to sugar maple and beech. When older stands are cut and the initial density of pin cherry is lower, the succession is towards quaking aspen and bigtooth aspen, yellow birch and paper birch. On lower elevations in New England and south through the Appalachians, the succession is to the White Pine-Northern Red Oak-Red Maple, White Pine, Red Spruce, or Red Spruce-Fraser Fir types, or to the northern hardwood types *(14)*.

Pin cherry growth is rapid, and it is not uncommon for trees growing on better sites in the central Appalachians to reach 20 to 25 cm (8 to 10 in) in diameter in 25 years (fig. 2) *(25)*. Pin cherry rarely persists in eastern upland hardwood forests in the United States for more than 35 years *(2)*.

Annual biomass production, including belowground material, in 6-year-old stands of pin cherry was about 1660 g/m^2 (0.34 lb/ft^2), which is higher than production in other temperate climate forests *(22)*.

Rooting Habit—Once a seedling attains a height of about 1 m (3 ft), lateral roots begin rapid growth *(17)*. In New England, root systems in 4- to 14-year-old stands were found to be shallow, generally not over 36 cm (14 in) deep, and to have many lateral branches *(23)*. In West Virginia, root systems of wind-thrown trees 25 years old were found to be confined to the upper 61 cm (24 in) of soil *(25)*. New shoots can arise from pieces of root left in the soil following site disturbance. Root cuttings, about 10 cm (4 in) in length, rooted 33 percent when incubated in soil under favorable greenhouse conditions *(17)*.

Reaction to Competition—Pin cherry is classed as very intolerant of shade. Early height growth is rapid, and where there is a high concentration of buried seed to produce seedlings after cutting or burning, pin cherry usually is dominant over all other vegetation.

In dense stands, the canopy closes in about 3 years, shading out many of the early intolerant species. After 25 to 30 years, sugar maple, beech, and in the northernmost regions, balsam fir are the seral species. At intermediate densities, pin cherry may be codominant with yellow birch, paper birch, and quaking aspen. At low densities, dominance is shared by many species including blackberries, striped maple, paper and yellow birch, quaking aspen, and stump sprouts of cut trees *(23)*.

Damaging Agents—Many diseases attack pin cherry during its short life. The most common leaf disease is cherry leaf spot, *Coccomyces hiemalis*, which is recognized by purplish to brown shot holes in the leaves that eventually cause yellowing of leaves and premature leaf fall. Repeated attacks reduce tree vigor. Other leaf spots on pin cherry are caused by *Cercospora circumscissa*, *Coryneum carpophyllum*, and three species of *Phyllosticta*. Additional pin cherry diseases are powdery mildew, *Podosphaera oxyacanthae* var. *tridactyla*; rust, *Tranzschelia pruni-spinosae*; and leaf curler, *Taphrina cerasi*.

The most widespread and commonly observed disease of pin cherry is black knot, *Apiosporina morbosa* *(31)*. Extensive trunk rot in the East is caused by *Fomes pomaceus*. This decay delignifies the wood, which then becomes soft, stringy, and discolored with brown flecks and streaks *(18)*.

Most of the important insects that attack pin cherry are leaf feeders, but because of the low ecomomic value of pin cherry, they are considered unimportant. A major leaf feeder is the uglynest caterpillar, *Archips cerasivoranus* (Fitch) and occasionally the eastern tent caterpillar, *Malacosoma americanum* *(17,30)*. Other leaf feeders are the cherry leaf beetle, *Pyrrhalta cavicollis*, a relative of the elm leaf beetle; Bruce spanworm, *Operophtera bruceata*; fall cankerworm, *Alsophila pometaria*; and a web-spinning sawfly, *Neurotoma fasciata* *(4)*. Many other insects attack *Prunus*, but there are only a few references to their attacks on pin cherry.

Special Uses

Twenty-five species of nongame birds, several upland game birds, fur and game mammals, and small mammals eat pin cherry fruit. Buds are eaten by upland game birds, especially sharp-tailed and

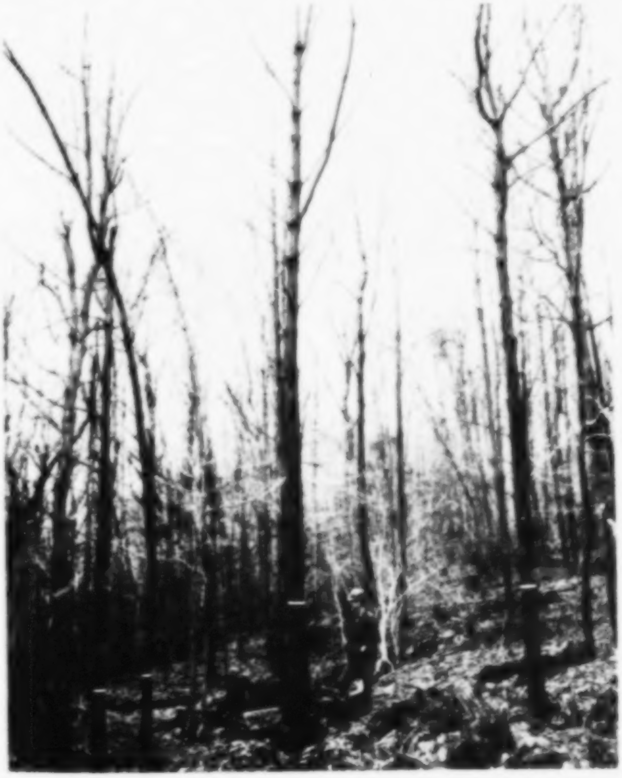

Figure 2—*Twenty-year-old pin cherry trees on the Fernow Experimental Forest, near Parsons, WV.*

ruffed grouse. Foliage and twigs are browsed by deer. However, the foliage has a high calcium to phosphorous ratio which is undesirable for good deer nutrition. Except in dense thickets, pin cherry provides only fair nesting cover and materials for birds. Beavers cut pin cherry and may completely remove small stands *(12)*. Leaves are poison (hydrocyanic acid) to livestock under certain conditions. However, the toxicity of pin cherry leaves is lower than that of most other cherry species *(17)*.

Because of its early place in succession and its rapid growth, pin cherry is important for minimizing losses of nutrients from an ecosystem. The rapid development of early successional species, such as pin cherry, channels water from runoff to evapotranspiration, thereby reducing erosion and nutrient loss; modifies the microclimate which reduces the rate of decomposition of litter and production of soluble ions; and incorporates into the developing biomass nutrients that do become available *(22)*.

In general, pin cherry is not used for lumber and is considered a noncommercial species. It occurs in abundance, however, over a wide range of sites and produces large quantities of biomass in a relatively short time. The species has been described as well adapted to intensive management and chip harvesting on short rotations for fiber and fuel *(13)*. At least one paper company accepts pin cherry along with other hardwood species in West Virginia *(8)*. Undoubtedly, it is also mixed with hardwoods in other areas.

In the nursery trade, pin cherry has been used as a grafting and budding stock for sour cherry *(12,29)*.

Genetics

One variety has been described in Canada, *Prunus pensylvanica* var. *mollis (5)*.

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Prunus serotina Ehrh. Black Cherry

Rosaceae Rose family

David A. Marquis

Black cherry *(Prunus serotina)*, the largest of the native cherries and the only one of commercial value, is found throughout the Eastern United States. It is also known as wild black cherry, rum cherry, and mountain black cherry. Large, high-quality trees suited for furniture wood or veneer are found in large numbers in a more restricted commercial range on the Allegheny Plateau of Pennsylvania, New York, and West Virginia *(36,44)*. Smaller quantities of high-quality trees grow in scattered locations along the southern Appalachian Mountains and the upland areas of the Gulf Coastal Plain. Elsewhere, black cherry is often a small, poorly formed tree of relatively low commercial value, but important to wildlife for its fruit.

Habitat

Native Range

Black cherry (figs. 1, 2) grows from Nova Scotia and New Brunswick west to Southern Quebec and Ontario into Michigan and eastern Minnesota; south to Iowa, extreme eastern Nebraska, Oklahoma, and Texas, then east to central Florida. Several varieties extend the range: Alabama black cherry (var. *alabamensis)* is found in eastern Georgia, northeastern Alabama, and northwest Florida with local stands in North and South Carolina; escarpment cherry (var. *eximia*) grows in the Edwards Plateau region of central Texas; southwestern black cherry (var. *rufula)* ranges from the mountains of Trans-Pecos Texas west to Arizona and south into Mexico; capulin black cherry (var. *salicifolia)* is native from central Mexico to Guatemala and is naturalized in several South American countries.

Climate

Black cherry and its varieties grow under a wide range of climatic conditions. In the heart of the commercial range on the Allegheny Plateau of Pennsylvania and New York, the climate is cool, moist, and temperate with average annual precipitation of 970 to 1120 mm (38 to 44 in) well distributed throughout the year. Summer precipitation averages 510 to 610 mm (20 to 24 in), and the frost-free growing season is 120 to 155 days. Winter snowfalls average 89 to 203 cm (35 to 80 in), and 45 to 90 days have snow cover of 2.5 cm (1 in) or more. Mean annual potential evapotranspiration approximates 430 to 710 mm (17 to 28 in), and mean annual water surplus is 100 to 610 mm (4 to 24 in). January temperatures average a maximum of 1° to 6° C (34° to 43° F) and a minimum of -11° to -6° C (12° to 22° F). July temperatures average a maximum of 27° to 29° C (80° to 85° F) and a minimum of 11° to 16° C (52° to 60° F) *(42)*.

Soils and Topography

Throughout its range in eastern North America, black cherry grows well on a wide variety of soils if summer growing conditions are cool and moist. In Canada it grows near sea level, whereas in Appalachian coves it exists at elevations up to 1520 m (5,000 ft) or more *(36)*. Best development occurs on the Allegheny Plateau at elevations of 300 to 790 m (1,000 to 2,600 ft).

On the Allegheny Plateau, black cherry develops well on all soils except for the very wettest and very driest *(36)*. There seem to be no major changes in site quality between soils developed from glacial till and those of residual origin. Black cherry tolerates a wide range of soil drainage. It grows about the same on well-drained sites as on somewhat poorly drained sites but shows rapid loss in productivity with increasingly wetter conditions *(6,12)*. The dry soils of ridge tops and of south- and west-facing slopes are less favorable for black cherry than the moist soils of middle and lower slopes on north and east exposures *(15,36)* though these effects are much less pronounced on the Allegheny Plateau than in the steep topography of the Appalachians.

Though great diversity exists, most of the forest soils important to black cherry are very strongly acid, relatively infertile, and have high, coarse fragment content throughout their profile. Kaolinite is the dominant clay mineral and is responsible for relatively low cation exchange properties *(14)*. The bulk of the upland soils have textures that range from sandy loam to silty clay loam, and many soils have developed fragipans that impede drainage and restrict root growth *(6,12,59)*. The large majority of upland soils are classified as Inceptisols or Ultisols according to present taxonomy, but Alfisols are also frequently present in colluvial landscape positions *(59,75)*.

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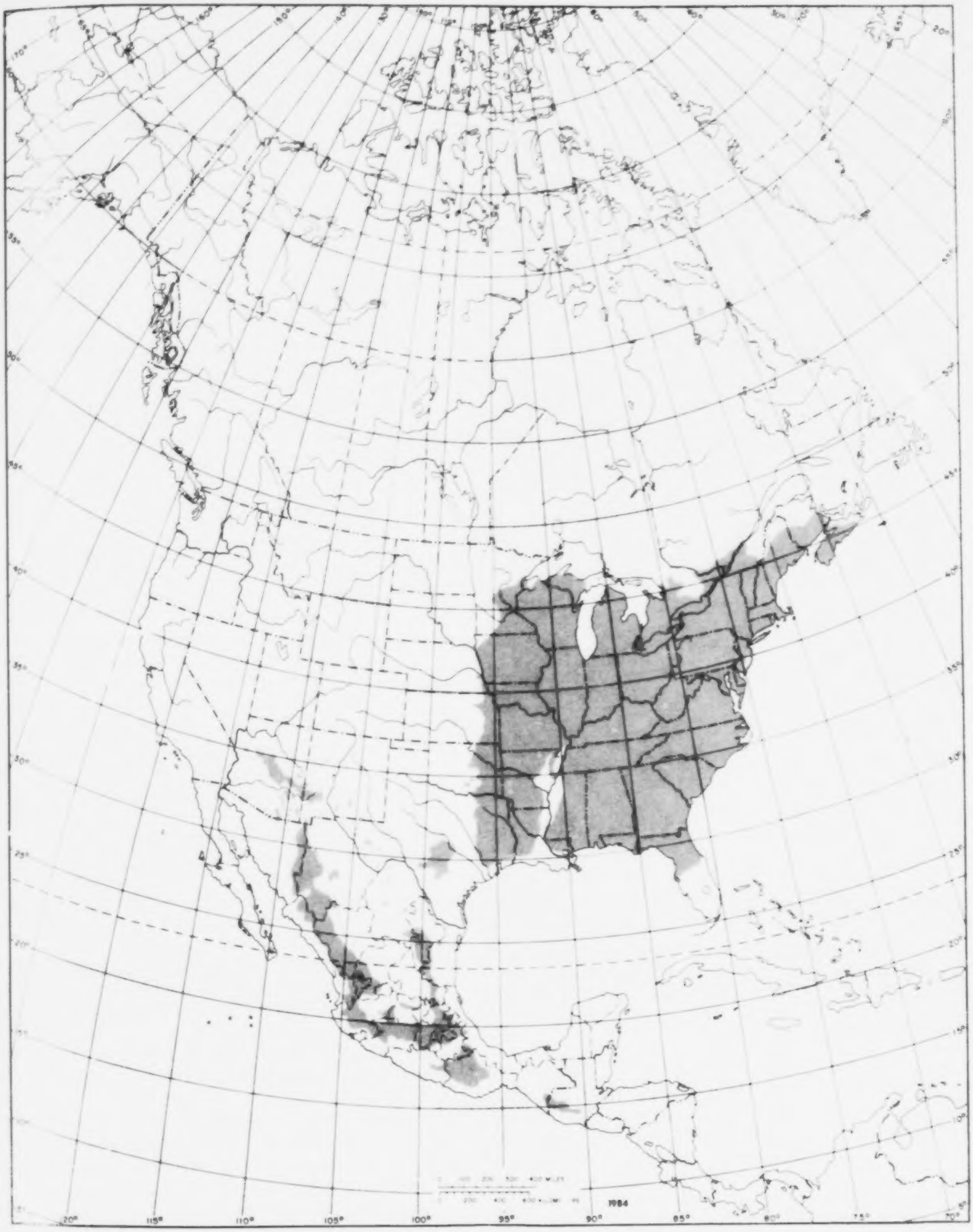

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Figure 1—*The native range of black cherry.*

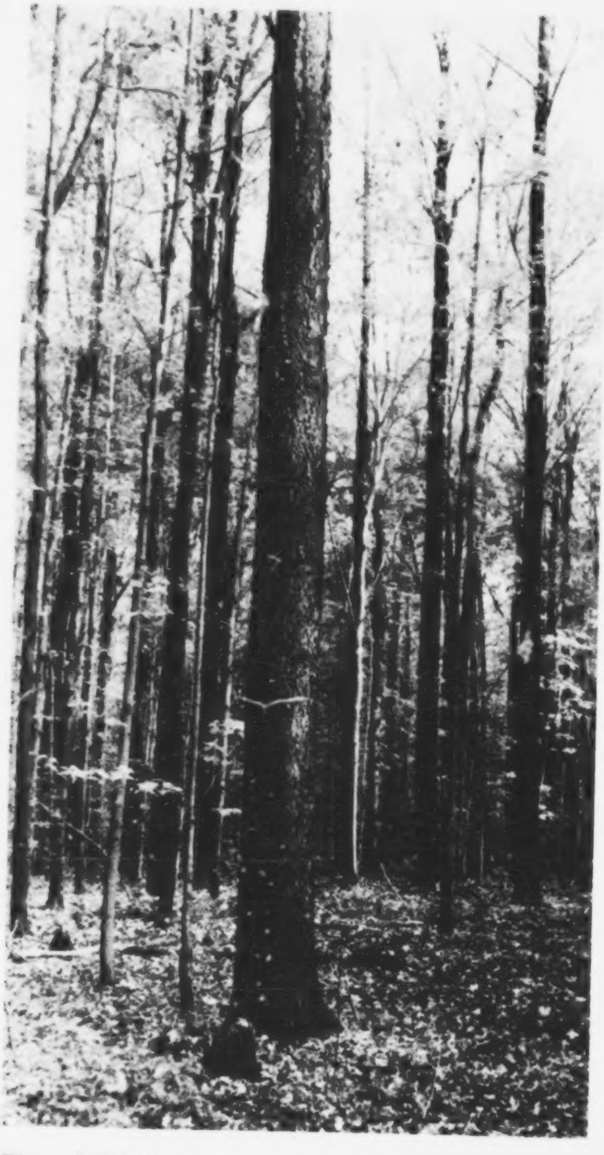

Figure 2—*Black cherry.*

Further southward throughout the Appalachian Highlands, black cherry generally grows on good to excellent sites as a scattered individual in association with other mesophytic hardwoods *(36,74)*, and sometimes in nearly pure stands at high elevations on soils with impeded drainage. In the Lake States, black cherry prefers deep, well-drained soils and is adversely affected by increasingly poorer soil drainage *(9)*.

Associated Forest Cover

Throughout the eastern United States, black cherry is a component of many forest cover types *(18)*. It is primarily a northern hardwood species, occurring as a common associate in most cover types of this group. Northern hardwood stands that contain large amounts of black cherry are recognized as a separate type: Black Cherry–Maple (Society of American Foresters Type 28) is found in the Allegheny Plateau and Allegheny Mountain sections of Pennsylvania, New York, Maryland, and West Virginia.

Black cherry is also found as a minor component of pine and hemlock types and other northern hardwood types in the Northern Forest Region, as well as upland oaks and other central types in the Central Forest Region. Black cherry is mentioned as a component of the following types:

14	Northern Pin Oak
17	Pin Cherry
19	Gray Birch–Red Maple
20	White Pine–Northern Red Oak–Red Maple
21	Eastern White Pine
22	White Pine–Hemlock
23	Eastern Hemlock
25	Sugar Maple–Beech–Yellow Birch
28	Black Cherry–Maple
31	Red Spruce–Sugar Maple–Beech
43	Bear Oak
44	Chestnut Oak
51	White Pine–Chestnut Oak
52	White Oak–Black Oak–Northern Red Oak
55	Northern Red Oak
57	Yellow-Poplar
59	Yellow-Poplar–White Oak–Northern Red Oak
60	Beech–Sugar Maple
64	Sassafras–Persimmon
108	Red Maple
109	Hawthorn
110	Black Oak

Other tree associates of black cherry in addition to those mentioned in the type names include white ash *(Fraxinus americana)*, cucumbertree *(Magnolia acuminata)*, sweet birch *(Betula lenta)*, American basswood *(Tilia americana)*, butternut *(Juglans cinerea)*, scarlet oak *(Quercus coccinea)*, balsam fir *(Abies balsamea)*, quaking and bigtooth aspens *(Populus tremuloides* and *P. grandidentata)*, American elm and rock elm *(Ulmus americana* and *U. thomasii)*. Important small tree associates include striped maple *(Acer pensylvanicum)*, pin cherry *(Prunus pensylvanica)*, eastern hophornbeam *(Ostrya virginiana)*, American hornbeam *(Carpinus caroliniana)*, and downy serviceberry *(Amelanchier arborea)*. Shrubs common in forest stands that contain significant amounts of black cherry include witch-hazel (*Hamamelis virginiana*), hobblebush (*Viburnum alnifolium*), and various other viburnums. Hay-scented fern (*Dennstaedtia punctilobula*), New York fern (*Thelypteris noveboracensis*), shorthusk grass (*Bracheylytrum erectum*), violets (*Viola* spp.), wood sorrel (*Oxalis* spp.), asters (*Aster* spp.), and club mosses (*Lycopodium* spp.) are also prevalent in the understory in many areas.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Unlike domestic cherries, which flower before the leaves appear, black cherry flowers late in relation to leaf development. At the latitude of 41° to 42° N. in Pennsylvania and New York, black cherry flowers usually appear around May 15 to May 20. At that time, the leaves are nearly full-grown though still reddish in color (*36*). Flower development in other parts of the range varies with climate—from the end of March in Texas to the first week of June in Quebec, Canada.

Black cherry flowers are white, solitary, and borne in umbel-like racemes. The flowers are perfect and are insect pollinated (*22*). Several species of flies, a flower beetle, and several species of bees, including the honey bee, work the blossoms for pollen and nectar. Self-pollination has been observed, but none of the self-pollinated flowers developed into viable seeds (*21*).

Late spring frosts may damage the flowers before they open, and frosts occasionally cause large numbers of newly set fruits to fall from the pedicels without maturing (*36*). Premature dropping of green fruits is also a problem in some years. The fruit is a one-seeded drupe about 10 mm (0.38 in) in diameter with a bony stone or pit. The fruit is black when ripe.

Seed Production and Dissemination—Limited flowering of black cherry seedlings in a seed orchard has been observed a few years after planting (*5*). Viable seeds have been produced on open-grown seedlings or sprouts as young as 10 years of age and on trees as old as 180 years. However, the period of maximum seed production in natural stands is generally between 30 and 100 years of age (*36*). Some individual trees never produce significant quantities of seed even when they reach an age and crown position where it is expected.

In most stands of seed-bearing age, some seeds are produced nearly every year. Good crops occur at intervals of 1 to 5 years across the geographic range of black cherry; on the Alleghany Plateau of northwestern Pennsylvania, good crops have occurred about every other year (*7,23*). On the Allegheny Plateau, fruit ripening and seedfall occur between August 15 and mid-September; the time is earlier in the southern range and later in the northern range. In the southeastern United States, fruits ripen in late June and seedfall is complete by early July. There may be as much as 3 weeks difference in fruit maturation dates between trees growing in the same stand.

Cleaned black cherry seeds range from 6,800 to 17,900/kg (3,100 to 8,100/lb), averaging 10,600/kg (4,800/lb). Seed weight varies geographically, with larger seeds in the northwest range and smaller seeds in the south and east.

The bulk of the seed crop falls to the ground in the vicinity of the parent tree. Circles of advance seedlings beneath scattered cherry trees and an absence of seedlings elsewhere are common occurrences in closed stands. As a result, the amount of black cherry advance reproduction is highly dependent on the number and distribution of seed-producing trees in the overstory (*7*). Songbirds distribute modest quantities of seeds in their droppings or by regurgitation. Omnivorous mammals, such as foxes and bears, also distribute seeds in their droppings. Bird and mammal distribution often accounts for a surprising abundance of advance cherry seedlings in stands lacking cherry seed producers.

Seedling Development—Black cherry seeds require a period of after-ripening before germination will take place (*22*). Under natural conditions, this occurs during winter months in the forest floor. The usual pattern is for seeds of 1 year's crop to germinate over the following 3 or more years (*45,77*). Because of frequent seed crops and delayed germination, often a considerable quantity of viable cherry seeds is stored in the forest floor beneath cherry stands, freeing natural regeneration from dependency on current seed production (*45*).

At the time of germination, the endosperm swells and splits the stone into two halves. Contrary to some beliefs, germination does not depend upon splitting of the seed coat by frost, or partial decomposition of the bony seed coat by soil organisms, or being passed through the digestive tract of birds. Germination is hypogeous; that is, the cotyledons remain below the soil surface (*22*).

Seedbed requirements for germination are not rigid. Mineral soil is not required. In fact, germination is somewhat less on mineral soil than on undisturbed humus or leaf litter (*37,43*). Few seeds germinate in areas that have had the organic horizons stripped off or that are compacted by logging machinery. A moist seedbed is required for good germination, and burial of seeds to a depth of several inches is beneficial, apparently because it provides a stable moisture supply. Shade also improves germination by helping to maintain stable moisture. Germination is best beneath a canopy that represents 60 percent stocking or more, and germination decreases at lower canopy densities and is poorest in full sunlight *(43,47)*.

Under a forest canopy, myriads of cherry seedlings start in the vicinity of seed trees practically every year. Many of these survive 3 or 4 years even under the dense shade of an uncut stand, but few grow to be more than 12 or 15 cm (5 or 6 in) tall or survive more than 5 years under that low level of light. Nevertheless, those that die are quickly replaced by newly germinated seedlings, so a fairly dense understory of small black cherry seedlings is often present under seed-producing stands of black cherry. Where canopy density has been reduced by partial cutting, cherry advance seedlings survive longer and grow taller in response to the higher level of light *(47,49)*. Overstory stocking levels of 50 to 70 percent provide optimum conditions for establishment of black cherry advance reproduction *(48)*. Good germination and high survival provide for maximum seedling numbers at this level, and seedling heights of 0.3 to 0.6 m (1 to 2 ft) are achieved in about 5 years. Best height growth of established seedlings, however, occurs in full sunlight *(43,49)*.

Black cherry seedlings reach a height of 5 to 10 cm (2 to 4 in) within 30 days of germination. Under dense shade they do not grow much more, averaging less than 3 cm (1 in) of growth per year until they die because of lack of light. In the open, cherry stems have the potential to grow faster than most associated species. Juvenile height growth often averages 46 cm (18 in), and a few individuals may grow 91 cm (36 in) or more per year. With fertilization, annual terminal growth of 1.2 to 1.8 m (4 to 6 ft) is common; growth of up to 2.4 m (8 ft) per year has been observed on some trees *(1)*.

Seedlings typically develop a taproot with numerous laterals during the first few years. Under adequate light, the roots penetrate 15 to 20 cm (6 to 8 in) the first year in most soils. Well before black cherry reaches sapling size, a spreading form of root system develops in which a distinct taproot is no longer evident *(36)*.

Black cherry advance seedlings more than 15 cm (6 in) tall and at least 2 years old survive well and grow rapidly after exposure to full sunlight. Smaller seedlings survive in somewhat lower numbers, but they can be important sources of regeneration too. Smaller seedlings survive better if they grow under a partially cut canopy before release rather than under an uncut canopy *(53)*.

A two-cut shelterwood sequence provides the best conditions for the establishment and subsequent growth of black cherry regeneration. The seed cut should reduce the overstory to 50 or 60 percent relative density to provide for establishment of a large number of seedlings of modest size. A removal cut 5 to 10 years later releases the established seedlings for rapid growth and development *(49)*. In some stands, adequate numbers of advance seedlings are present naturally, and the overstory removal or clearcut can be made without an earlier seed cut *(25)*. The presence of advance seedlings is critical, however, and clearcutting may not regenerate cherry in stands where advance seedlings are lacking, especially where deer browsing, interfering plants, or other factors limit reproduction *(55,56)*.

Some black cherry seedlings do become established after removal cutting, and these supplement those that originated as advance seedlings. But direct exposure to sunlight is not conducive to best germination. For this reason, small clearcut patches or strips often provide better regeneration than large block clearcuts *(36)*, except where advance seedlings are adequate by themselves.

In stands where all species start at the same time, cherry quickly overtops tolerant species *(51)*. Under partial shade, however, height growth of cherry is often less than that of its tolerant associates *(48)*, and cherry is far less likely to grow into the main canopy through small gaps created by removal of a single tree. As a result, single-tree selection cutting generally discriminates against black cherry reproduction *(46)*.

Vegetative Reproduction—Black cherry readily sprouts from stumps and the sprouts grow rapidly, especially in full sunlight. Small, suppressed seedlings that have been released from overhead shade but which are bent or broken by logging operations will produce well-formed sprouts from the root collar *(63)*. These seedling sprouts are an important and highly desirable source of regeneration. Even large old stumps sometimes are capable of sprouting; a 258-year-old, 122-cm (48-in) d.b.h. black cherry sprouted when cut. Maximum sprouting occurs in trees less than 40 or 50 years of age however. Clearcuttings of very young second growth cherry stands has resulted in third growth cherry stands in which more than half of the trees were of sprout origin *(36)*.

Sprouts of cherry tend to have poorer form than comparable seedlings but grow faster than seedlings during the first 20 to 30 years. Although trees of seedling or seedling-sprout origin are preferred for timber production, usually several stems of each sprout clump are capable of growing into high-quality sawtimber *(41,78)*. The incidence of butt rot from the parent stump is not as great in black cherry sprouts from stumps as large as 25 cm (10 in) in diameter or from stumps that have been overgrown by their sprouts by 35 years of age *(8)*. Thus, sprouts of good form originating low on the stump are not discriminated against in silvicultural operations.

Sapling and Pole Stages to Maturity

Growth and Yield—Black cherry grows very fast in the seedling, sapling, and pole stages, generally outgrowing and overtopping common associates such as sugar maple and beech. This gives rise to even-aged stands that are distinctly stratified into crown layers and diameters based on species. Black cherry generally occupies the dominant and codominant crown strata, while sugar maple and beech occupy an intermediate or suppressed crown position. Where present, species of intermediate tolerance such as red maple and white ash tend to be intermediate in crown position and size between the cherry and the sugar maple and beech. In stands where tolerant sugar maple and beech are present in the dominant crown positions alongside black cherry, the tolerants are often residuals of the previous stand that had a distinct head start on the cherry *(51)*.

Black cherry maintains its growth advantage over associated species for 60 to 80 years, so the proportion of the basal area or volume in cherry tends to increase over time in mixed stands. By age 60, codominant red maple diameter growth is often as good as or better than that of codominant cherry. Beyond age 80 to 100 years, diameter growth slows, mortality of cherry increases rapidly, and the importance of the species in the stand declines. However, few stands of such age are available to judge the rapidity with which cherry disintegrates at advanced ages. Site index curves for black cherry on the Allegheny Plateau have recently been developed *(2)*.

Average annual diameter growth of black cherry dominants and codominants might be 0.65 cm (0.25 in) between ages 10 and 40 years, 0.5 cm (0.20 in) between ages 40 and 70 years, and 0.4 cm (0.15 in) between ages 70 and 100 years.

Growing space requirements for black cherry are considerably lower than for the associated species (except for hemlock) *(71)*. Thus, stands containing a high percentage of black cherry carry more basal area and more volume per acre than stands with a low percentage of cherry. For example, full stocking for stands with a quadratic average stand diameter of 25 cm (10 in) is 31.7 m^2 of basal area per hectare (138 ft^2/acre) if there is 20 percent cherry, and 42.2 m^2 (184 ft^2) if there is 80 percent cherry. Maximum stocking also varies with stand diameter. Stocking is 31.7, 37.0, and 40.4 m^2/ha (138, 161, and 176 ft^2/acre) at average quadratic stand diameters of 15, 25, and 35 cm (6, 10, and 14 in), respectively, for stands with 50 percent cherry *(67,72)*.

Rooting Habit—The root system of black cherry is predominantly spreading and shallow, even in well-drained soils. Most roots are restricted to the upper 60 cm (24 in) of soil or less, with occasional sinker roots extending to depths of 90 to 120 cm (36 to 48 in). On wet sites, the tendency toward shallow rooting is especially pronounced. Because of this tendency to grow taller than associated species in mixed stands, cherry is vulnerable to windthrow, especially on poorly drained soils and at older ages *(36)*.

Reaction to Competition—Black cherry is classed as intolerant of shade. Although black cherry seedlings are common under uncut stands and survive for 3 to 5 years, they do not live for extended periods or move up into larger size classes without moderate to heavy opening of the overstory canopy.

In sapling and larger sizes, black cherry trees are considered very intolerant of competition. Cherry trees are found primarily in the dominant and codominant crown classes. Those individuals that drop to lower crown levels decline in growth and soon die. Thus, diameter distribution of black cherry in even-aged stands follows the bell-shaped curve typical of intolerant species *(51)*.

Black cherry dominants and codominants respond to thinning with slight to moderate increases in diameter growth, especially at ages up to 50 or 60 years *(17,36,54)*. But thinning does not generally produce a response in trees that have been suppressed. Even early thinnings and cleanings intended to elevate intermediate or suppressed cherry to codominate crown positions generally have failed *(13,73)*.

Even-aged silviculture best satisfies the silvical requirements for black cherry regeneration, using either clearcutting where advance seedlings are already present or shelterwood cutting to develop them where they are absent *(56,58)*. Advance seedlings and seed stored in the forest floor generally make retention of seed trees unnecessary. Uneven-aged silviculture, especially single-tree selection, tends to gradually eliminate cherry from the stands, because cherry does not move up into the dominant canopy without at least moderate levels of sunlight *(46)*. Group selection cutting might maintain small percentages of cherry in uneven-aged stands, though this has never been demonstrated clearly.

Damaging Agents—The most important defoliating insects attacking black cherry include the eastern tent caterpillar *(Malacosoma americanum)* and the cherry scallop shell moth *(Hydria prunivorata)* *(3)*. Infestations of these insects are sporadically heavy, with some apparent growth loss and occasional mortality if heavy defoliations occur several years in a row.

Attacks by numerous species of insects cause gum defects in black cherry, resulting in reduced timber quality. Gum spots in the wood are often associated with the Agromyzid cambium miner *(Phytobia pruni)*, the peach bark beetle *(Phloeotribus liminaris)*, and by the lesser peachtree borer *(Synathedon pictipes)* *(35,40,66)*. A wide variety of insects can cause injury to terminal shoots of black cherry seedlings and saplings, resulting in stem deformity. *Archips* spp. and *Contarinia cerasiserotinae* are among the more important *(64)*.

The most common disease is cherry leaf spot caused by *Coccomyces lutescens* *(36)*. Large numbers of black cherry seedlings are sometimes weakened or killed by this disease. Repeated attacks reduce the vigor of larger trees. Most other foliage diseases cause little damage.

Black knot, a native disease caused by the fungus *Apiosporina morbosa* is common on black cherry *(27)*. It causes elongated rough black swellings several times the diameter of the normal stem. Small twigs may be killed within a year after infection. Large cankerous swellings, a foot or more in length, may occur on the trunks of larger trees, and where several such lesions are scattered along the bole, the tree is worthless for lumber. *Cytospora leucostoma* is the cause of a canker disease responsible for widespread branch mortality of black cherry in Pennsylvania *(26)*. Common infection courts are decaying fruit racemes and bark fissures caused by excessive gum production following passage of the larvae of *Phytobia pruni*, a cambium mining insect.

Several basidiomycete fungi that cause root and butt rot of living black cherry trees include *Armillaria mellea, Coniophora cerebella, Polyporus berkeleyi*, and *Tyromyces spraguei*. Many other fungi cause decay of the main trunk; these include *Fomes fomentarius, Fomitopsis pinicola, Poria prunicola. P. mutans*, and *Laetiporus sulphureus* *(29,36)*. Damage caused by glaze storms exposes black cherry to infection by top-rot fungi *(16)*.

Porcupines girdle and kill black cherry trees and also consume bark, thereby providing entry points for fungi. Meadow mice and meadow voles girdle the stem near the ground *(37)*. Such damage where grass or other herbaceous cover provides suitable habitat for the mice is probably one of the major causes of planting failure in unregenerated clearcuts and old fields.

White-tailed deer, rabbits, and hare feed on black cherry seedlings *(36)*. In parts of Pennsylvania, deer browsing is the most serious problem of black cherry. Reproduction sometimes is completely eliminated by browsing, and most regeneration cuts are affected by reduced stocking, delays in establishment, and shifts in species composition toward less palatable beech and striped maple *(50,57)*. Damage is dramatic after clearcutting, but damage to advance reproduction also is important.

In areas of high deer population such as Pennsylvania, successful reproduction can be assured only where advance seedlings are so abundant that deer cannot eat all of them in the few years required for them to grow out of reach *(55,57)*. Black cherry fares somewhat better than associated species such as sugar maple, red maple, white ash, and yellow-poplar, which are preferred deer browse. Where successful regeneration develops after clearcutting in this region, it is often nearly pure black cherry. Guidelines and techniques for regenerating stands with black cherry have been developed *(56,58)*.

Cherry is somewhat more vulnerable to storm damage than many of its associates because it often towers above the general canopy in mixed stands. Sapling and pole-sized trees are frequently bent by glaze or wet snow, causing loss of the leader and severe crooks that make them unsuitable for sawtimber. Cherry trees make remarkable recovery after breakage, however, with little loss of diameter growth. Decay spreads more slowly in cherry than in some of the associated species, so long-term effects are less severe than they seem to be at first *(36,65)*.

Cherry trees of all sizes are highly susceptible to fire injury. Even large trees are killed by moderate to severe fire, but most resprout unless the fire was unusually hot. Black cherry is intolerant of flooding. Of 39 species studied in a Tennessee flood test, black cherry was the most sensitive to high water *(28)*.

Certain herbaceous plants interfere with establishment of black cherry regeneration through an allelopathic mechanism. Flat top aster *(Aster umbellatus)*, rough stemmed goldenrod *(Solidago rugosa)*, brackenfern *(Pteridium aquilinum)* and wild oatgrass *(Danthonia compressa)* *(30)* release chemicals from their leaves or roots that sometimes interfere with black cherry growth and development. Woodland fern and grasses may also interfere with black cherry regeneration, through a complex of mechanisms that involve both light and nitrogen effects *(31,34)*. Black cherry may interfere with regeneration of other tree species, such as red maple *(32)*, but this has not been investigated thoroughly.

Special Uses

Black cherry fruits are an important source of mast for many nongame birds, squirrel, deer, turkey, mice and voles, and other wildlife. The leaves, twigs, and bark of black cherry contain cyanide in bound form as the cyanogenic glycoside, prunasin *(33)*. During foliage wilting, cyanide is released and domestic livestock that eat wilted foliage may get sick or die *(38)*. Deer eat unwilted foliage without harm *(36)*.

The bark has medicinal properties. In the southern Appalachians, bark is stripped from young black cherries for use in cough medicines, tonics, and sedatives *(36,39)*. The fruit is used for making jelly and wine. Appalachian pioneers sometimes flavored their rum or brandy with the fruit to make a drink called cherry bounce. To this, the species owes one of its names—rum cherry *(36)*.

Genetics

Several varieties of black cherry have been recognized in the southern portion of the range: var. *alabamensis*, Alabama black cherry; var. *eximia*, escarpment cherry; var. *rufula*, southwestern black cherry or Gila chokecherry; and var. *salicifolia*, the capulin black cherry *(36)*.

Population Differences

Provenance testing of black cherry has identified several traits that are related to geographic origin. Seed weight seems to exhibit a definite clinal pattern, increasing as latitude increases *(11,60,62)*. The largest seeds are found among the northern sources (especially those from Wisconsin); seed weight generally decreases to the south and east *(60)*. For example, weight of northwestern Pennsylvania seeds is consistently lower than that of West Virginia seeds *(62)*. Elevation also affects seed weight, with heavier seeds coming from the higher elevations *(19)*. Differences in stem form, branching habit, and incidence of black knot infection of seedlings have also been observed among seed sources *(10)*.

Growth and survival of cherry seedlings are likewise affected by seed source *(4,11,76)*. Seedlings from southern sources and lower elevations break dormancy sooner and suffer more severe frost damage than seedlings from northern sources and higher elevations when planted in the North or at higher elevations. Conversely, growth is better from southern sources and lower elevations. An interesting exception seems to be cherry from the heart of the commercial range in northwestern Pennsylvania that outgrew local sources when outplanted in West Virginia during the first 10 years of the USDA Forest Service's tree improvement program.

There is also great variation within sources. Large variation in growth of seedlings within half-sib families is common *(70)*, and open pollinated superior trees have not produced significantly better progeny than average trees *(61)*. Considerable variations also exist in such attributes as tendency to produce epicormic sprouts when drastically exposed, and time of leaf senescence in the autumn.

Races and Hybrids

The four subspecies or varieties of black cherry mentioned above may be considered as races. There are no recognized interspecific hybrids with black cherry. There is one account of controlled hybridization between wild black cherry and one of the varieties—the capulin black cherry *(80)*.

There is conflicting evidence on the possibility of polyploidy in black cherry. Most reports indicate that the chromosome number of black cherry is $2n=32$, which makes it a tetraploid. However, one report using material from Tennessee indicates the presence of a nontetraploid population there *(20)*.

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Quercus alba L. White Oak

Fagaceae Beech family

Robert Rogers

White oak (*Quercus alba*) is an outstanding tree among all trees and is widespread across eastern North America. The most important lumber tree of the white oak group, growth is good on all but the driest shallow soils. Its high-grade wood is useful for many things, an important one being staves for barrels, hence the name stave oak. The acorns are an important food for many kinds of wildlife.

Habitat

Native Range

White oak (figs. 1, 2) grows throughout most of the Eastern United States. It is found from southwestern Maine and extreme southern Quebec, west to southern Ontario, central Michigan, to southeastern Minnesota, south to western Iowa, eastern Kansas, Oklahoma, and Texas; east to northern Florida and Georgia. The tree is generally absent in the high Appalachians, in the Delta region of the lower Mississippi, and in the coastal areas of Texas and Louisiana.

The west slopes of the Appalachian Mountains and the Ohio and central Mississippi River Valleys have optimum conditions for white oak, but the largest trees have been found in Delaware and Maryland on the Eastern Shore.

Climate

White oak grows under a wide variety of climatic conditions. Mean annual temperature ranges from 7° C (45° F) along the northern edge of the growing area to nearly 21° C (70° F) in east Texas and north Florida. The extreme low temperature ranges from -46° C (-50° F) in Wisconsin and Minnesota to -18° C (0° F) in north Florida. Annual precipitation ranges from 2030 mm (80 in) in the southern Appalachians to 760 mm (30 in) in southern Minnesota. Snowfall averages 178 cm (70 in) in southern Maine and less than 3 cm (1 in) in northern Florida. The average noon July relative humidity is less than 50 percent in the western part of the range and more than 65 percent on the Atlantic Coast. The frost-free season is 5 months in the north and 9 months in the extreme southern part of the range. The mean maximum frost penetration in the soil is 102 cm (40 in) in the north and 3 cm (1 in) in the south.

The optimum range of white oak in the Ohio Valley and central part of the Mississippi Valley has the following average climatic conditions: annual temperature, 13° C (55° F); annual precipitation, 1020 mm (40 in); annual snowfall, from 38 to 51 cm (15 to 20 in); noon relative humidity in July, 55 percent; frost-free season, 6 months; and frost penetration, 25 cm (10 in) *(28)*.

Soils and Topography

White oak grows on a wide range of soils and sites. It is found on podzols, gray-brown podzolic soils, brown podzolic soils, red and yellow podzolic soils, lithosols, planasols, and alluviums. The tree grows on both glaciated and nonglaciated soils derived from many parent materials. It is found on sandy plains, gravelly ridges, rich uplands, coves, and well-drained loamy soils. Growth is good on all but the driest, shallowest soils *(28)*.

Mineral nutrition is not limiting to white oak growth except on very sandy soils where moisture is also a limiting factor. The amount of variability in white oak growth that can be accounted for by soil factors alone is low *(9,28,37)*. Nevertheless, several studies have identified the more important factors to be thickness of the A_1 and A_2 horizons and the percent clay in the surface soils *(18,25,28)*. White oak is most frequently found growing on soils in the orders Alfisols and Ultisols.

The major site factors influencing white oak growth are latitude, aspect, and topography *(9,18)*. White oak has the ability to grow on all upland aspects and slope positions within its range except extremely dry, shallow-soil ridges; poorly drained flats; and wet bottom land. It grows best on north- and east-facing lower slopes and coves and grows well on moderately dry slopes and ridges with shallow soils. White oak is more abundant although smaller in size on the drier west- and south-facing slopes than on the more mesophytic sites.

It is found at all altitudes in the central and southern parts of its range, but it is seldom found above 150 m (500 ft) in elevation in the northern part of its range. It is excluded from the high Appalachians in New York and New England; but it is a scrub tree at elevations of 1370 m (4,500 ft) in the southern Appalachians *(28)*.

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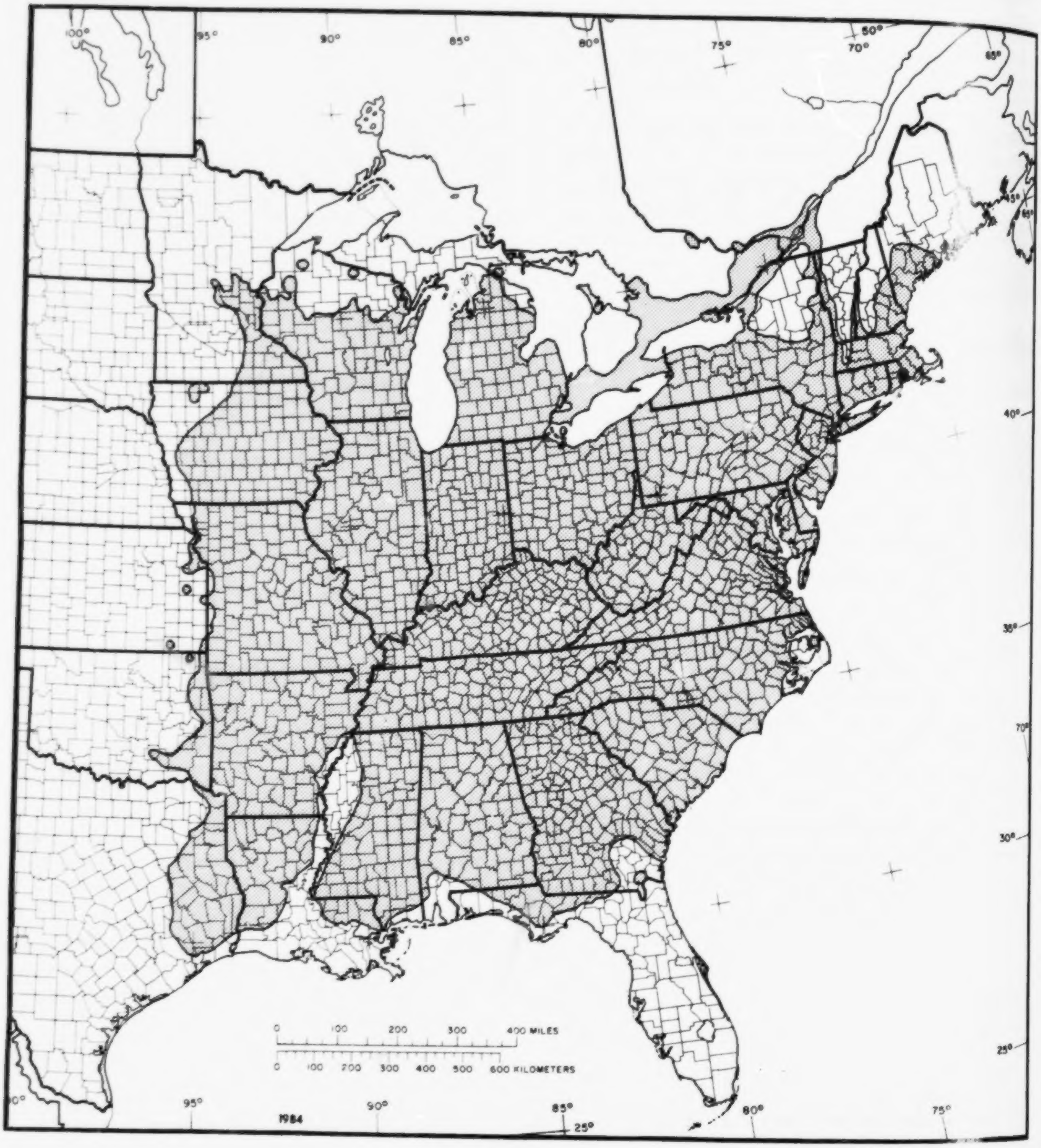
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Figure 1—*The native range of white oak.*

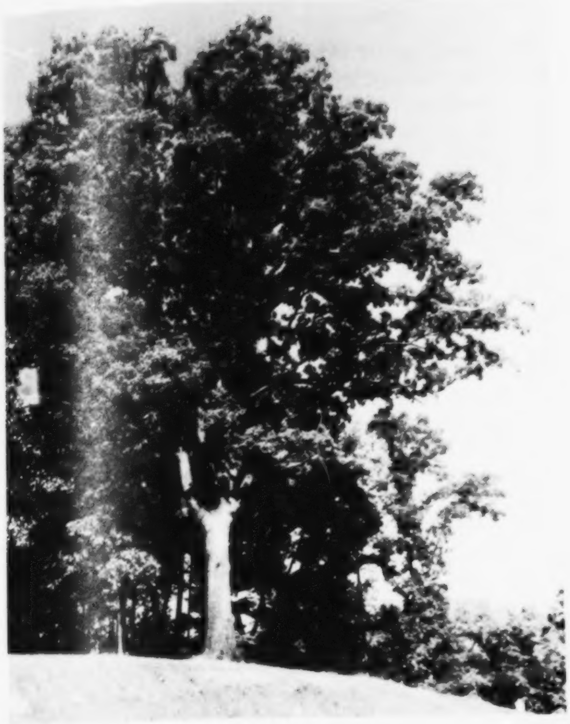

Figure 2—*White oak.*

Associated Forest Cover

White oak grows in association with many other trees, the more important of which are other upland oaks (*Quercus* spp.), hickories (*Carya* spp.), yellow-poplar (*Liriodendron tulipifera*), American basswood (*Tilia americana*), white ash (*Fraxinus americana*), sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), shortleaf pine (*Pinus echinata*), loblolly pine (*P. taeda*), eastern white pine (*P. strobus*), and eastern hemlock (*Tsuga canadensis*). The most frequent associates are other oaks and the hickories.

White oak is a major component of three forest cover types (*10*): White Oak–Black Oak–Northern Red Oak (Society of American Foresters Type 52), White Oak (Type 53), and Yellow-Poplar–White Oak–Northern Red Oak (Type 59). It is a minor component of the following 28 other forest types:

Northern Forest Region

14 Northern Pin Oak
19 Grey Birch–Red Maple
21 Eastern White Pine
22 White Pine–Hemlock
23 Eastern Hemlock
26 Sugar Maple–Basswood
27 Sugar Maple
51 White Pine–Chestnut Oak
60 Beech–Sugar Maple

Central Forest Region

40 Post Oak–Blackjack Oak
42 Bur Oak
43 Bear Oak
44 Chestnut Oak
45 Pitch Pine
46 Eastern Redcedar
55 Northern Red Oak
57 Yellow-Poplar
58 Yellow-Poplar–Eastern Hemlock
61 River Birch–Sycamore
110 Black Oak

Southern Forest Region

75 Shortleaf Pine
76 Shortleaf Pine–Oak
78 Virginia Pine–Oak
79 Virginia Pine
80 Loblolly Pine–Shortleaf Pine
81 Loblolly Pine
82 Loblolly Pine–Hardwood
91 Swamp Chestnut Oak–Cherrybark Oak

Life History

Reproduction and Early Growth

Flowering and Fruiting—White oak flowers in the spring at about the same time leaves appear. The time may vary from late March to late May depending upon latitude. It is monoecious; flowers of both sexes are present on the same tree. The yellowish staminate flowers appear first and are borne in 5- to 8-cm (2- to 3-in) catkins. The reddish pistillate flowers appear 5 to 10 days later either singly or in pairs on short stalks. Female flowers that are not fertilized abscise during the development period. High abscission rates are common and may be related to weather conditions during the period of pollination, ovule development, and fertilization (*44*). Ripe anthers open and close with changes in relative humidity. Normally, pollen dissemination is completed within 3 days but periods of wet weather delay pollen shedding. Dry winds and freezing weather are also detrimental to flower development and pollen shedding (*28*). Acorn crops are good in years when the weather is warm for 10 days during flowering and then cool for 13 to 20 days afterward. The acorn crop has been poor in years when cool periods preceded warm periods at the time of flowering (*36*).

Acorn maturity is reached approximately 120 days after pollination. Acorn drop follows 25 days later and is complete within a month. Physiological maturity, as indicated by normal germination, is reached when acorns change color from green to light brown *(4)*. Acorns germinate almost immediately after falling to the ground in September or October.

Seed Production and Dissemination—White oak can produce seeds prolifically, but good acorn crops are irregular and occur only every 4 to 10 years. Sometimes several years may pass without a crop. Acorn yields range from 0 to 500,000 acorns per hectare (202,000/acre) *(7,22,28)*. This great variation in acorn production exists not only among isolated stands of oaks but also among individual trees within stands and from year to year.

Trees normally bear seeds between the ages of 50 and 200 years, sometimes older; however, open-grown trees may produce seeds as early as 20 years. Individual white oak trees tend to have either very good or very poor seed crops and are noticeably consistent in seed production from year to year *(20,28,36,40)*. A recent study *(13)* showed that white oak flower production varies not only annually but also among trees within a given year and that much of the variation in acorn production can be related to flower abundance at the time of pollination. More than 23,000 acorns were produced during a good seed year by an individual white oak tree growing in Virginia; it was 69 years old, 63.5 cm (25 in) in d.b.h., and 21 m (69 ft) tall, and had a crown area of 145 m^2 (1,560 ft^2). Average production in good years for individual forest-grown trees, however, is probably no more than 10,000 acorns.

Several studies have shown that only a small portion of the total mature acorn crop (sometimes only 18 percent) is sound and fully developed; the remainder is damaged or destroyed by animals and insects *(15,28,40)*. However, some damaged acorns germinate if the embryo is not damaged. Light acorn crops are often completely destroyed by animals and insects, so seedlings are produced only during heavy crop years.

Seeds are disseminated by rodents (chiefly squirrels and mice), gravity, and wind. The area seeded by individual trees is small and therefore widespread reproduction depends on adequate distribution of seedbearing trees.

Seedling Development—Germination is hypogeal. Sound white oak acorns have a germination capacity between 50 and 99 percent *(30)*. Seeds germinate in the fall soon after dropping, requiring no pretreatment for germination. For germination to occur, the moisture content of acorns must not fall below 30 to 50 percent. Germination is favored at soil temperatures between 10° and 16° C (50° and 60° F). Germination is severely limited after 15 days of exposure to flooded conditions *(1)*. When acorns germinate, their roots begin to grow but the shoot remains dormant. This trait serves to protect it from damage by freezing *(11)*.

After germination, root growth continues until interrupted by cold weather. Broken radicles are replaced on freshly sprouted seeds. Root and shoot growth resumes in the spring, and after the first growing season, seedlings 7.6 to 10.2 cm (3 to 4 in) high normally develop a large taproot 6 to 13 mm (0.25 to 0.50 in) in diameter and more than 30.5 cm (12 in) long.

Oak seedling establishment is best on loose soil because the radicle cannot penetrate excessively compact surfaces. A humus layer is especially important because it keeps the soil surface loose and porous and because it mechanically supports the acorn as the radicle penetrates the soil *(28)*.

If climate and soil are favorable for germination, white oak reproduces adequately from seed when: (1) large seed trees are within about 61 m (200 ft); (2) litter cover is light to moderate (but not thick); and (3) light reaching seedling level is at least 35 percent of full sunlight. Reproduction is least abundant on moist sites that have a thick carpet of ferns and lesser vegetation *(6)*. Seedlings persist more readily in open stands typical of dry exposures but can be maintained on moist sites if adequate sunlight reaches the forest floor.

Although important, soil moisture is probably not a critical factor in determining early seedling survival except under unusually dry conditions. At least one study has shown that when available soil moisture was 19 percent of oven dry soil weight, white oak seedling survival was 98 percent; at 3 percent available moisture, survival was 87 percent *(28)*.

A Missouri study has shown that despite an adequate crop of sound acorns, the number of new white oak seedlings produced in any given year is low compared to other oaks, particularly black oak *(Quercus velutina)*. However, these individuals may persist in the understory for many years (90 years) by repeatedly dying back and resprouting. This phenomenon permits the gradual buildup of advance reproduction that is often taller and more numerous than the advance reproduction of associated oaks.

Under ideal growing conditions it is common for individual seedlings to grow 0.6 m (2 ft) or more a year. However, white oak seedlings established at the time of overstory removal normally grow too slowly to be of value in stand reproduction. Mean height of seedlings 10 years after overstory removal on sites with a site index of 13 to 19 m (43 to 63 ft) at base age 50 years in Missouri was slightly more than 0.6

m (2 ft) while seedling sprouts and stump sprouts averaged 4.9 and 6.4 m (16 and 21 ft), respectively *(27)*.

Vegetative Reproduction—Small white oak trees sprout prolifically and vigorously when cut or damaged by fire. The ability to sprout depends on the d.b.h. of the parent trees as follows *(23)*:

D.b.h. class		Stumps likely to sprout
cm	*in*	*percent*
5 to 14	2 to 5	80
14 to 29	6 to 11	50
29 to 42	12 to 16	15
42–	16–	0

Shoot elongation of stump sprouts increases with increasing stump diameter up to 15 cm (6 in) after which it declines. Annual height growth of stump sprouts when overstory competition is removed averages 0.7 m (2.2 ft) *(24)*.

Another source of vegetative reproduction is seedling sprouts. Seedling sprouts are stems with root systems that are several to many years older. These develop as a result of repeated dieback or mechanical damage.

In general, low stump sprouts from pole-size trees and seedling sprouts are about as good as trees grown from seed. However, sprouts originating high on the stump are likely to have heartwood decay *(28)*.

The seedlings and seedling sprouts already present in a mature stand (advance reproduction), together with stump sprouts, regenerate the stand with oaks following overstory removal. Although many stands may have adequate numbers of stems, the size of the reproduction when the overstory is removed is the key to adequate growth and subsequent stocking *(31)*. A minimum of 1,095 stems per hectare (443/acre) that are 1.37 m (4.5 ft) tall or taller is required to ensure a future stocking of at least 546 dominant and codominant oaks per hectare (221/acre) when average stand diameter is 7.6 cm (3 in) *(33)*. Nevertheless, stands deficient in advance reproduction may be adequately stocked if a sufficient number of stumps sprout.

Sapling and Pole Stages to Maturity

Growth and Yield—White oak is a large, long-lived tree often 24 to 30 m (80 to 100 ft) in height and 91 to 122 cm (36 to 48 in) in d.b.h. Individual trees 46 m (150 ft) high, 244 cm (96 in) in d.b.h., and 600 years old have been recorded. In the open it is characterized by a short stocky bole with a wide-spreading rugged crown. In the forest, white oaks develop a tall straight trunk with a compact crown *(28)*.

White oak generally has the reputation of being a slow-growing tree. According to growth averages from Forest Resources Evaluation data in the Central States, 10-year d.b.h. growth of white oak was 3.0 cm (1.20 in) for seedlings and saplings, 3.5 cm (1.37 in) for poles, and 4.7 cm (1.84 in) for sawtimber. These growth rates were slower than scarlet oak (*Quercus coccinea*), northern red oak (*Q. rubra*), or black oak but faster than chestnut oak (*Q. prinus*). Among the non-oak species only hickory and beech had slower growth rates than white oak, while yellow-poplar, black walnut (*Juglans nigra*), white ash, and sugar maple all had faster growth rates than white oak *(16)*.

Although white oak was once a component of mixed, uneven-aged stands, most white oaks today are in pure to mixed second growth stands of sprout origin. Individual trees may contain 5.7 m^3 (1,000 fbm) or more of wood but this is uncommon. Pure and mixed unthinned stands at age 80 normally contain from 28 to 168 m^3/ha (2,000 to 12,000 fbm/acre) of wood, occasionally more. Mean annual volume growth over a 60-year period in these stands ranges from 0.95 m^3/ha on fair to poor sites to 2.2 m^3/ha on good sites (68 fbm/acre to 156 fbm/acre) *(17)*. Total volumes of fully stocked, even-aged stands of mixed oak have been reported to be 89.3 m^3/ha (6,380 ft^3/acre) at age 100 on site index 24.4 m (80 ft) sites; and merchantable volumes of 294 m^3/ha (21,000 fbm/acre) have been found in stands on comparable sites in Wisconsin at age 100. However, such high volumes are rare and occur in localized areas *(28)*.

Because oaks in general, and white oak specifically, are long-lived trees, rotation length can be long (120+ years). But rotation lengths can be shortened by as much as 50 percent and yields increased dramatically if stands are thinned early and regularly, particularly on good sites. If thinnings are begun at age 10 and stands rethinned to 60 percent stocking at 10-year intervals, volume yield at age 60 on good sites (264 m^3/ha or 18,840 fbm/acre) is approximately double that in similar unthinned stands. Mean annual growth in such thinned stands is 3.9 m^3/ha (279 fbm/acre) *(17)*.

Throughout its range, site index for white oak is generally less than for yellow-poplar and other important oaks on the same site *(26,28)*. White oak site index is approximatley 1.2 m (4 ft) less than black oak and 2.1 m (7 ft) less than scarlet oak. On all sites the index for white oak is higher than that for shortleaf pine. And on the poorest sites, the index for white oak is higher than that for yellow-poplar.

Rooting Habit—White oak is deep rooted—a trait that persists from youth to maturity. White oak seedlings produce a conspicuous, well-developed taproot but this gradually disappears with age and is replaced by a fibrous root system with well-developed, tapered laterals. Although the deepest point of root penetration observed during a study conducted at the Harvard Black Rock Forest in Massachusetts approached 1.2 m (4 ft), most of the main branches away from the central stem were within 53.3 cm (21 in) of the ground surface. Fine roots are typically concentrated in dense mats in the upper soil horizons usually close to trunks but occasionally lying beneath the base of neighboring trees *(5,14,39)*.

Root grafts between neighboring trees are common, especially under crowded conditions.

The ratio between the area of the root system and the area of the crown ranges from 3.4 to 1 to 5.8 to 1.

Following stand thinning, roots of released trees are capable of elongating at the rate of 0.24 m (0.8 ft) per year.

Root regeneration of young forest-grown seedlings may be hampered following top damage. A study of root regeneration of 1-0 white oak seedlings growing under greenhouse conditions has shown that new growth of seedlings whose shoot tops were pruned was 20 to 80 percent less than that of unpruned seedlings *(12)*.

Reaction to Competition—White oak is generally classed as intermediate in tolerance to shade. It is most tolerant in youth and becomes less tolerant as the tree becomes larger. White oak seedlings, saplings, and even pole-size trees are nevertheless able to persist under a forest canopy for more than 90 years.

Saplings and pole-size trees respond well to release. A 41 percent increase in diameter has resulted in young stands 1 year following release, and this trend has continued through the fourth year following release. Moreover, diameter growth of released trees for a 20-year period can be expected to be double that of nonreleased trees. Release significantly increases height growth only for those trees in the intermediate or suppressed crown classes. Young white oak sprout clumps thinned to one stem show a slightly greater diameter growth response over released single-stemmed trees *(8,28,29)*. Such increases are possible when stands are heavily thinned, but the response becomes less dramatic as residual stand stocking increases. Other things being equal, however, the trees to release should be the large potential crop trees that show evidence of rapid recent growth.

Thinning combined with fertilization can boost 2-year diameter growth by 95 percent over unthinned and unfertilized pole-size white oak according to tests conducted in the Boston Mountains of Arkansas *(19)*. The addition of nitrogen and calcium to soils in the Allegheny Plateau region of central Pennsylvania increased stand volume more than 40 percent *(42)*.

White oak usually becomes dominant in the stand because of its ability to persist for long periods of time in the understory, its ability to respond well after release, and its great longevity. When associated with other oaks and hickory in the central and southern hardwood forests, white oak is considered a climax tree. On good sites in the north, it is usually succeeded by sugar maple. In the Ozark-Ouachita Highlands, white oak is climax on moderately dry to moist sites. In sheltered, moist coves and well-drained second bottoms throughout its range it may be succeeded by beech and other more tolerant species *(10)*.

Most research and field experience suggest that even-aged silviculture is most suitable for white oak growing in pure or mixed hardwood stands. Although selection silviculture has been considered, it has been difficult to develop a sustainable stand structure without continual cultural treatments to restrain the more tolerant species, particularly on the better sites *(34)*.

If oak advance reproduction is adequate, clearcutting is the recommended silvicultural system *(32)*. If oak advance reproduction is scarce or absent, new seedlings need to be established. Some reduction of overstory density should help to stimulate seed production, but because of the periodicity of seed crops, it will probably take a long time to establish an adequate number of new seedlings. Seedlings can be planted under an overstory and allowed to develop. The overstory should be maintained at about 60 percent stocking and if competition from an existing understory will impair the growth of the planted seedlings, its density should be reduced. Planting oaks after clearcutting has generally been unsatisfactory because the planted seedlings do not grow fast enough to compete with new sprouts. Reducing both overstory and understory competition is likely to accelerate the growth of small oak advance reproduction. However, even with this increased growth, advance oak reproduction grows slowly and the development period may be from 10 to 20 years or longer.

Natural pruning of white oak is usually good in moderately to heavily stocked stands. Large dominant trees have cleaner boles than smaller trees in lower crown classes. Some branches along the trunk tend to persist when exposed to sunlight.

Epicormic sprouting may be heavy on trees that have been grown in fully stocked stands for 20 years or more and then given sudden and heavy release *(28)*. However, residual stand density and the vigor of trees may be more important to the persistence of epicormics than to their initiation following thinning *(41)*. Significantly more epicormic branches have been observed on multiple-stemmed trees than on single-stemmed trees.

Live branches not more than 4 cm (1.5 in) in d.b.h. may be saw-pruned without danger of introducing rot. However, epicormic sprouts will often develop around the edges of the wound on saplings and small pole-size trees. Diameter growth of thinned and pruned trees may be 10 percent less than thinned but unpruned trees *(35)*.

Damaging Agents—Several insects attack white oak trees *(15,28,43)*. They are usually not important but may become epidemic and kill weakened trees. Economically, the most important are the wood borers. These may damage the wood of standing trees and cause log and lumber defects.

White oak is attacked by several leaf eaters including the gypsy moth *(Lymantria dispar)*, orangestriped oakworm *(Anisota senatoria)*, variable oakleaf caterpillar *(Heterocampa manteo)*, several oak leaf tiers *(Psilocorsis* spp.), and walkingstick *(Diapheromera femorata)*. Frequently trees are killed from an interaction of damaging agents such as a defoliator followed by invasion of a shoestring fungus and the twolined chestnut borer *(Agrilus bilineatus)*.

White oak also hosts various scale insects, gall-forming insects, and twig pruners, but most of these are of minor importance. White oak acorns are commonly attacked by insects, in some cases affecting half the total acorn crop. Weevils of the genera *Curculio* and *Conotrachelus* cause most acorn damage. Light acorn crops usually are more heavily infested than heavy ones. Two moths damage acorns, the filbertworm *(Melissopus latiferreanus)* and *Valentinia glandulella*. The Cynipid wasps cause galls to develop in the acorn or on the cup.

The oak timberworm *(Arrhenodes minutus)* frequently damages white oak, making it unfit for tight cooperage. Attacks by this insect usually occur at wounds made by logging, lightning, and wind. Golden oak scale *(Asterolecanium variolosum)* can seriously damage and even kill the tree. It is especially damaging when accompanied by drought.

Decay of heartwood resulting from fire scars causes the most serious white oak losses. The amount of decay depends on the size of the wound, the species of fungi, and the length of time since wounding. In general, rot spreads in the stem if the basal scar is more than 0.3 m (1 ft) in d.b.h. The larger the wound, the faster the rot *(28)*.

Oak wilt, a vascular disease caused by the fungus *Ceratocystis fagacearum*, is potentially the most destructive disease of both the red and white oaks. It is widely distributed throughout the Central States. White oak is less susceptible to oak wilt than the red oak species, and may lose only a limb at a time, or may sustain infection by the pathogen without ever showing symptoms *(21)*.

Several other diseases of white oak seldom kill or cause much loss. Perennial cankers induced by bark diseases *Strumella coryneoides* and *Nectria galligena* are responsible for most of the losses in white oak particularly where ice and snow accumulation is common. Damage results from a weakening of the bole at the cankers with subsequent wind breakage. The trunk can become wholly or partially unmerchantable.

A root rot caused by the fungus *Armillaria mellea* attacks weakened trees. Root rot caused by *Armillaria tabescens* is similar and attacks oaks in the South. White root rot caused by *Inonotus dryadeus* is common on weak and suppressed trees.

The fungus *Gnomonia veneta* causes irregular brown areas on leaves and shoots. It may cause loss of some leaves and rarely, complete defoliation.

Oak leaf blister, caused by *Taphrina caerulescens*, is prevalent on eastern oaks, producing blisterlike swellings on the foliage.

White oak is moderately resistant to ice breakage, sensitive to flooding, and resistant to salt spray and brief salt-water submergence *(21,28)*. It is sensitive to fire injury but less so than scarlet oak. Coal smoke and the resulting fly ash deposit on the soil surface substantially reduce white oak productivity *(2,38)*.

Special Uses

Acorns are a valuable though inconsistent source of wildlife food. More than 180 different kinds of birds and mammals use oak acorns as food; among them are squirrels, blue jays, crows, red-headed woodpeckers, deer, turkey, quail, mice, chipmunks, ducks, and raccoons. White oak twigs and foliage are browsed by deer especially in clearcuts less than 6 years old *(3)*.

White oak is sometimes planted as an ornamental tree because of its broad round crown, dense foliage, and purplish-red to violet-purple fall coloration. It is less favored than red oak because it is difficult to transplant and has a slow growth rate.

Genetics

In addition to the type variety, two varieties of *Quercus alba* have been named: *Q. alba* var. *repanda* Michx. and *Q. alba* var. *latiloba* Sarg.

Seven hybrids are recognized: *Quercus* × *jackiana* Schneid. (*Q. alba* × *bicolor*); *Q.* × *bebbiana* Schneid. (*Q. alba* × *macrocarpa*); *Q.* × *beadlei* Trel. (*Q. alba* × *michauxii*); *Q.* × *faxonii* Trel. (*Q. alba* × *prinoides*); *Q.* × *saulii* Schneid. (*Q. alba* × *prinus*); *Q.* × *fernowii* Trel. (*Q. alba* × *stellata*); *Q.* × *bimundorum* Palmer (*Q. alba* × *robur*).

White oak also hybridizes with the following: Durand oak (*Quercus durandii*), overcup oak (*Q. lyrata*), and chinkapin oak (*Q. muehlenbergii*).

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Quercus bicolor Willd. Swamp White Oak

Fagaceae Beech family

Robert Rogers

Swamp white oak *(Quercus bicolor)* is a medium-sized tree of the north central and northeastern mixed forests. It is found in lowlands, along edges of streams, and in swamps subject to flooding. It is rapid growing and long lived, reaching 300 to 350 years. The hard strong wood is commercially valuable and is usually cut and sold as white oak. Many kinds of wildlife eat the acorns, particularly ducks.

Habitat

Native Range

Swamp white oak, a lowland tree (figs. 1, 2), grows from southwestern Maine west to New York, southern Quebec, and southern Ontario, to central Michigan, northern Wisconsin, and southeastern

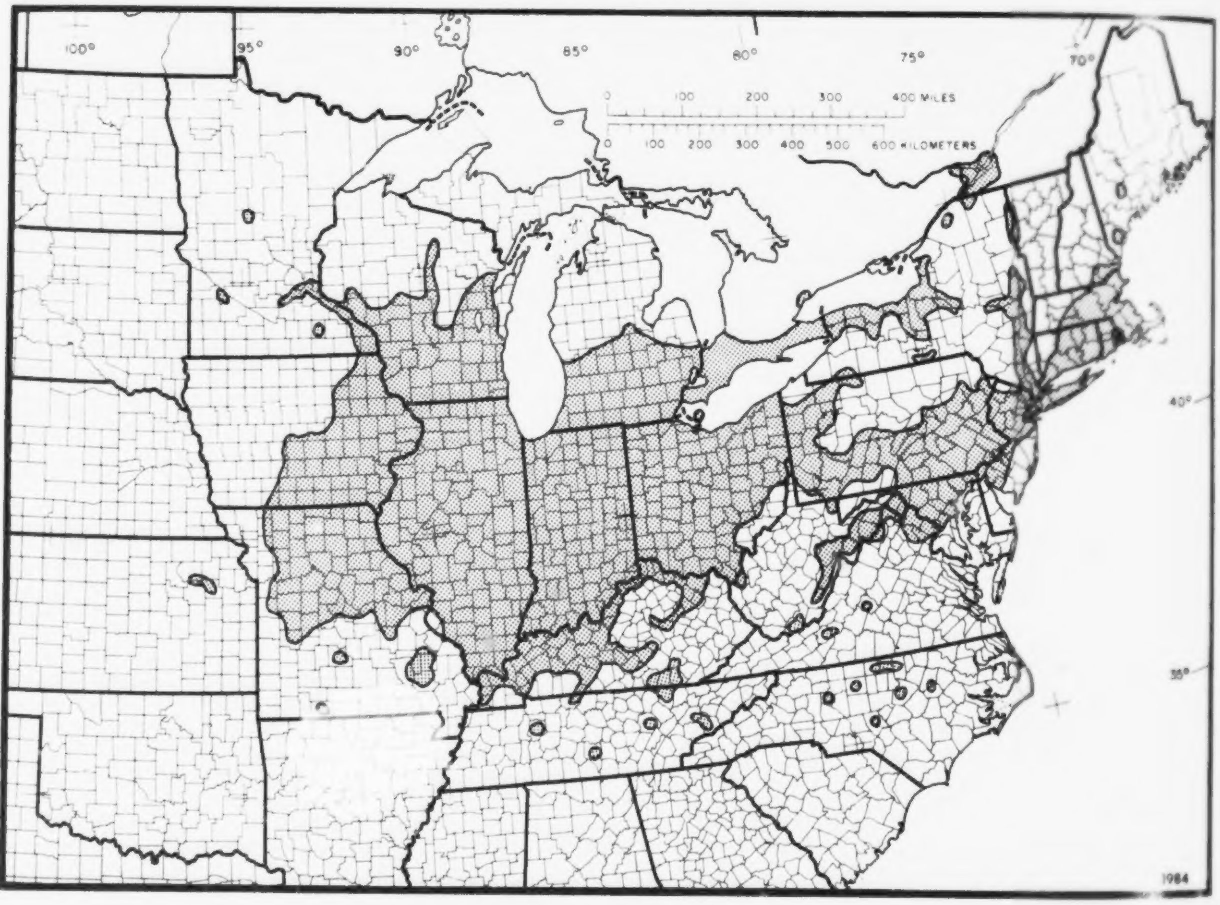

Figure 1—*The native range of swamp white oak.*

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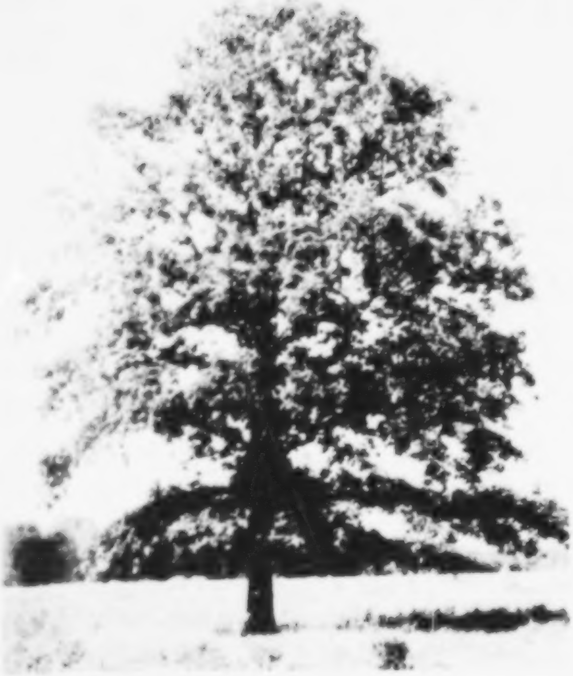

Figure 2—*Swamp white oak.*

Minnesota; south to Iowa and Missouri; east to Kentucky, Tennessee, Virginia, and New Jersey. It is scattered in North Carolina and northeastern Kansas. This species is most common and reaches its largest size in western New York and northern Ohio *(4)*.

Climate

Within the range of swamp white oak, mean annual temperatures vary from 16° C (60° F) in Arkansas to 4° C (40° F) in southern Ontario. Extremes in temperature vary from 41° C (105° F) to -34° C (-30° F). Average annual precipitation is from 640 mm (25 in) in southeast Minnesota to 1270 mm (50 in) in northeast Arkansas. The frost-free period ranges from 210 days in the southern part of the growing area to 120 days in the northern part *(4)*.

Soils and Topography

Throughout its range, swamp white oak is typically found on hydromorphic soils. These may be mineral soils that are imperfectly to poorly drained, as evidenced by high water tables and the presence of glei subsurface layers, or both; organic soils ranging from mucks (well decomposed) to peats (poorly decomposed) in which high water levels have favored organic accumulation; or alluvial soils underlain by a glei layer. These kinds of soils are associated with lands that are periodically inundated, such as broad stream valleys, low-lying fields, and the margins of lakes, ponds, or sloughs. Swamp white oak is not found where flooding is permanent *(2,4,5,6,8)*. In general, the soils on which this oak most commonly is found are in the orders Entisols and Inceptisols.

Associated Forest Cover

Swamp white oak is a consistent though mostly a minor component of hydromesophytic forest communities in which other species usually dominate. Tree species that commonly grow in association with swamp white oak are pin oak *(Quercus palustris)*, sweetgum *(Liquidambar styraciflua)*, red maple *(Acer rubrum)*, silver maple *(A. saccharinum)*, American elm *(Ulmus americana)*, eastern cottonwood *(Populus deltoides)*, sycamore *(Platanus occidentalis)*, green ash *(Fraxinus pennsylvanica)*, bur oak *(Quercus macrocarpa)*, shellbark and shagbark hickory *(Carya laciniosa* and *C. ovata)*, blackgum *(Nyssa sylvatica)*, black willow *(Salix nigra)*, and American basswood *(Tilia americana) (3,4,6)*.

Swamp white oak occurs in four forest cover types: Black Ash-American Elm-Red Maple (Society of American Foresters Type 39), Bur Oak (Type 42), Silver Maple-American Elm (Type 62), and Pin Oak-Sweetgum (Type 65). It is usually found singly in these types but occasionally may be abundant in small areas *(6)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Swamp white oak is monoecious; male and female flowers appear on the same tree in the spring at about the time leaves are one-third developed (May to June). The fruit, an acorn, matures in 1 year and is generally paired and borne on slender stalks from 3 to 8 cm (1.25 to 3.25 in) long. The ovoid acorns, each 19 to 32 mm (0.75 to 1.25 in) long and 13 to 19 mm (0.5 to 0.75 in) in diameter, fall during September and October.

Seed Production and Dissemination—Good crops of swamp white oak occur every 3 to 5 years, with light crops during intervening years. The minimum seed-bearing age is 20 years, optimum age is

75 to 200 years, and maximum age is usually 300 years. Because the seed of swamp white oak is not dormant, it germinates soon after falling. Seed collections should be made soon after ripening in order to delay early germination. These acorns are difficult to store without germination or loss of viability occurring. Sound acorns have a germinative capacity between 78 and 98 percent. Gravity, rodents, and water are the primary dispersing agents *(4,10)*.

Seedling Development—Germination is hypogeal *(10)*. After acorns germinate in the fall, roots continue to develop until growth is limited by low temperatures. Seedling establishment and early growth seem to be favored on the better drained lowland soils rather than on sites that are poorly drained or subjected to persistent flooding. In any case, adequate moisture and light are necessary for successful early development *(4,8)*.

Vegetative Reproduction—Like most oaks, swamp white oak produces seedling sprouts or stump sprouts when the top is cut or killed. The frequency of sprouting declines, however, with increasing d.b.h. *(8)*:

D.b.h. class		Stumps likely to sprout
cm	*in*	*percent*
15 to 27	6 to 10	75
27 to 39	11 to 15	30
39 to 52	16 to 20	10
52+	20+	5

Sapling and Pole Stages to Maturity

Growth and Yield—On the better drained lowland soils, the growth rate of swamp white oak is comparable to that of white oak. The root system is usually shallow, but the tree is relatively long lived—up to 300 years or more. Normally it is a medium-sized tree, 18 to 23 m (60 to 75 ft) in height and 61 to 91 cm (24 to 36 in) d.b.h., although trees up to 30 m (100 ft) tall and 213 cm (84 in) d.b.h. have been reported.

Swamp white oak normally grows in mixtures with other bottom-land species and is abundant only locally. Individual old growth trees may contain as much net volume as 3.4 m^3 (600 fbm) but this is uncommon *(4)*.

Rooting Habit—No information available.

Reaction to Competition—The tree is classed as intermediate in tolerance to shade, and seedlings become established under moderate shade. Lowland forests in which swamp white oak grows are characterized by instability and successional uncertainty because of the variable effects of flooding, together with the presence of saturated soils. Swamp white oak may achieve dominance on the better drained lowland soils together with basswood, northern red oak *(Quercus rubra)*, American beech *(Fagus grandifolia)*, and sugar maple *(Acer saccharum)* *(5)*. Once established, it is able to compete effectively with American elm, green ash, and black willow. Limited current evidence indicates clearcutting to be an adequate silvicultural system, particularly on the better sites *(2,8)*.

In forest stands swamp white oak has a straight bole with ascending branches and a narrow crown. However, open-grown trees are generally poorly formed and often have persistent lower branches *(4)*.

Damaging Agents—Windthrow may be a problem especially in recently thinned stands.

Disease and insects affecting swamp white oak are essentially the same as those found on white oak. Oak anthracnose can be damaging to individual trees but is generally not fatal. Swamp white oak is susceptible to the oak wilt fungus *(Ceratocystis fagacearum)* and in Illinois *Phomopsis* canker and *Coniothyrium* dieback were found on this oak. In addition, an *Alternaria* fungus was found on blighted petioles *(4,7)*.

Special Uses

The acorns are sweet, like others in the white oak group, and are eaten by squirrels and other rodents *(9)*. In a study in Wisconsin, swamp white oak acorns were found to make up 27 percent of the diet of wild ducks. Several nongame bird species include these acorns in their diet *(4)*.

Genetics

Two forms of swamp white oak have been described: a mesophytic form with leaves that are green and velvety on the lower surface and a more xerophytic form with leaves that are white-tomentulose beneath. The following six hybrids with swamp white oak are recognized: *Quercus* × *jackiana* Schneid. *(Q. bicolor* × *alba)*; *Q.* × *humidicola* Palmer *(Q. bicolor* × *lyrata)*; *Q.* × *schuettei* Trel. *(Q. bicolor* × *macrocarpa)* *(1)*; *Q.* × *introgressa* P. M. Thomson *(Q. bicolor* × *muehlenbergii* × *prinoides)* *(11)*; *Q.* × *substellata* Trel. *(Q. bicolor* × *stellata)*; *Q.* × *nessiana* Palmer *(Q. bicolor* × *virginiana)*. Swamp white oak also hybridizes with chestnut oak (*Quercus prinus*) and English oak (*Q. robur*).

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Quercus chrysolepis Liebm. Canyon Live Oak

Fagaceae Beech family

Dale A. Thornburgh

Canyon live oak (*Quercus chrysolepis*), also called canyon oak, goldcup oak, live oak, maul oak, and white live oak, is an evergreen species of the far West, with varied size and form depending on the site. In sheltered canyons, this oak grows best and reaches a height of 30 m (100 ft). On exposed mountain slopes, it is shrubby and forms dense thickets. Growth is slow but constant, and this tree may live for 300 years. The acorns are important as food to many animals and birds. The hard dense wood is shock resistant and was formerly used for wood-splitting mauls. It is an excellent fuel wood and makes attractive paneling. Canyon live oak is also a handsome landscape tree.

Habitat

Native Range

Canyon live oak (fig. 1) is found in the Coast Ranges and Cascade Range of Oregon and in the Sierra Nevada in California, from latitude 43° 85′ N. in southern Oregon to latitude 31° 00′ N. in Baja California, Mexico *(9,15)*. In southern Oregon, it grows on the interior side of the Coast Ranges and on the lower slopes of the Cascade Range. It grows throughout the Klamath Mountains of northern California, along the coastal mountains and the western slopes of the Sierra Nevada, and east of the redwood (*Sequoia sempervirens*) forest on the coast, except in the King Range, where it grows close to the coast. In central and southern California, canyon live oak is found on or near the summits of mountains. Scattered populations appear in the mountains of southern Nevada, Arizona, and northwestern Chihuahua, Mexico *(17)*.

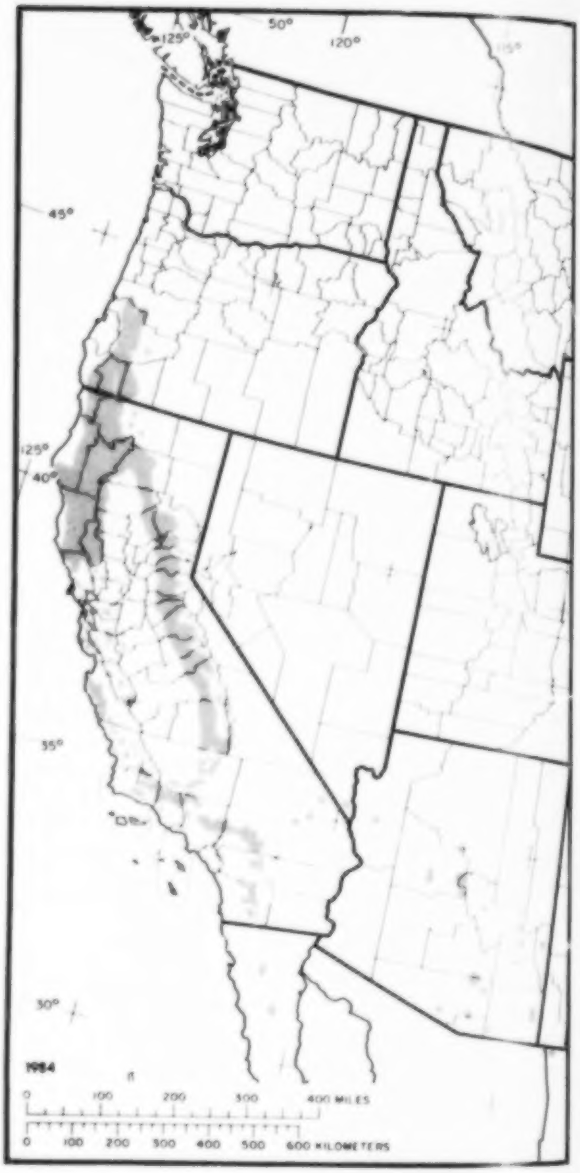

Figure 1—*The native range of canyon live oak.*

Climate

Populations of canyon live oak receive more than 2790 mm (110 in) of precipitation in the northern portion of their range to less than 300 mm (12 in) in southern California. Interior populations receive from 810 mm (32 in) in the Sierra Nevada to 150 mm (6 in) in the desert mountains. Most of the annual precipitation in the Coast Ranges and the Sierra Nevada is winter rain. In the desert mountains, half

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the precipitation is received in summer, the other half in winter.

In the northern portion of the range of canyon live oak, the mean temperature in summer ranges from 20° to 23° C (68° to 74° F) and in winter, from 3° to 5° C (37° to 41° F); in the southern portion, from 21° to 25° C (70° to 77° F) in summer and from 5° to 7° C (41° to 45° F) in winter. The frost-free period varies from 160 to 230 days throughout the range *(1)*.

Soils and Topography

Canyon live oak is found on many types of soil. In the northern part of its range, this oak often dominates on steep, shallow, rocky, infertile soils having little soil development. On deep, coarse-textured soils, canyon live oak is usually secondary in importance to Douglas-fir *(Pseudotsuga menziesii)* and tanoak *(Lithocarpus densiflorus)*. On deep, fine-textured soils, canyon live oak is normally a small shrub under an overstory canopy of associated species. In northwestern California, canyon live oak grows on sedimentary, metasedimentary, granitic, serpentine, and periodite parent materials. In southern California, it is a dominant on a broad range of soils from shallow and poorly developed to deep and well developed *(13)*. Canyon live oak is most commonly found on soils of the orders Inceptisols and Alfisols.

Canyon live oak grows at elevations of 488 to 1525 m (1,600 to 5,000 ft) in southwestern Oregon; in northern California, from 90 to 1370 m (300 to 4,500 ft); and in southern California, up to 2740 m (9,000 ft). As its name implies, canyon live oak is often the dominant tree on steep canyon walls. In areas of moderate to high precipitation, it is found on southerly aspects, and in the drier parts of its range, on northerly aspects.

Associated Forest Cover

In southwestern Oregon, canyon live oak is primarily associated with Douglas-fir, tanoak, giant chinkapin *(Castanopsis chrysophylla)*, and Pacific madrone *(Arbutus menziesii)* in the mixed evergreen forests. In these forests it is a codominant tree and a shrub in the *Pseudotsuga menziesii–Quercus chrysolepis–Lithocarpus densiflorus/Quercus chrysolepis–Lithocarpus densiflorus* climax community type. On steep canyon slopes, it is dominant in the *Quercus chrysolepis–Lithocarpus densiflorus–Pseudotsuga menziesii/Rhus diversiloba/* moss community. On benches and ridgetops, canyon live oak along with tanoak occupies the lower tree canopy of the *Pseudotsuga menziesii–Pinus* spp./*Lithocarpus densiflorus–Quercus chrysolepis–Castanopsis chrysophylla/Pteridium aquilinum* community. Canyon live oak also is a major codominant in the successional evergreen chaparral, along with hoary manzanita *(Arctostaphylos canescens)* and greenleaf manzanita *(A. patula)*. In the mixed conifer zone of the western slope of the Cascade Range, canyon live oak primarily grows in semipermanent fire chaparral associated with snowbrush ceanothus *(Ceanothus velutinus) (6)*.

In the Klamath region of northern California, canyon live oak is an occasional small tree or shrub throughout the *Abies concolor* zone of the montane or mixed conifer forest of the interior side of the Coast Ranges and Klamath Mountains. In the *Abies concolor/Arbutus menziesii/Corylus cornuta* type, canyon live oak is a codominant lower canopy tree under ponderosa pine, sugar pine, and white fir *(Abies concolor)*. The associated codominant lower canopy trees are giant chinkapin, bigleaf maple, and Pacific dogwood *(Cornus nuttallii) (10)*. It is also an understory tree in the *Abies concolor/Vicia americana, Abies concolor/Chimaphila umbellata, Abies concolor/Berberis nervosa,* and *Abies concolor/Ceanothus prostratus* types *(1)* and, at lower elevations, in the forest cover types Pacific Ponderosa Pine–Douglas-Fir (Society of American Foresters Type 244) and Pacific Ponderosa Pine (Type 245) *(5)*.

In the Coast Ranges of northern California, canyon live oak is a major component of the mixed evergreen forest or Douglas-Fir–Tanoak–Pacific Madrone (Type 234). In these forests, it is associated with bigleaf maple, California-laurel, coast live oak *(Quercus agrifolia)*, Douglas-fir, madrone, and tanoak. Canyon live oak is not usually found in the modal mixed evergreen community dominated by Douglas-fir and tanoak; however, it is dominant on steep, southwestern slopes associated with Douglas-fir and madrone in a *Quercus chrysolepis/Pseudotsuga menziesii* type. In the southern portion of the mixed evergreen forests, canyon live oak assumes more importance along with ponderosa pine. On serpentine soils, canyon live oak is a minor climax associate in the *Pinus ponderosa/Ceanothus cuneatus, Pseudotsuga menziesii/Corylus cornuta,* and *Lithocarpus densiflorus/Gaultheria shallon* types *(20)*.

In the central Coast Ranges of California, canyon live oak is a codominant in the mixed hardwood forests (Blue Oak–Digger Pine, Type 250), associated with coast live oak, blue oak *(Quercus douglasii)*, interior live oak *(Q. wislizeni)*, California black oak *(Q. kelloggii)*, madrone, tanoak, California laurel, and Digger pine *(Pinus sabiniana)*. In this area, it also occurs in successional chaparral associated with Eastwood manzanita *(Arctostaphylos glandulosa)*. At higher elevations, canyon live oak is dominant in the canyon live oak-Coulter pine forest (Canyon Live Oak, Type 249).

In the Sierra Nevada of California, canyon live oak is found in several forest types. In the low-elevation foothill woodland forest, it is occasionally found on steep, north-facing slopes associated with interior live oak, blue oak, and Digger pine. In the mixed oak woodland, canyon live oak is a codominant with interior live oak, along with a prominent understory of manzanita, toyon, and western poison-oak *(Rhus diversiloba)*. In the more mesic mixed oak forest, canyon live oak is a codominant with interior live oak, California black oak, bigleaf maple, and California-laurel *(17)*.

Above the foothill woodland zone, canyon live oak is a codominant in the mixed oak-evergreen forest where it associates with ponderosa pine, Douglas-fir, and California black oak. Still higher in elevation in the mixed conifer forest, canyon live oak occurs in small groves with an understory of poison-oak and swordfern *(Polystichum munitum)*, or in groves of mixed oak. It is also an understory small tree or shrub in the lower portion of the mixed conifer forests *(17)*.

In the Transverse Range of southern California, canyon live oak is an important subdominant of the yellow pine forest on steep, south-facing slopes where it associates with ponderosa pine, Jeffrey pine *(Pinus jeffreyi)*, and California black oak. In moister, cooler areas, canyon live oak is the major dominant in the stable bigcone Douglas-fir-canyon live oak forests *(13)*. Canyon live oak is also found in the western juniper woodlands where it is associated with Jeffrey pine, singleleaf pinyon *(Pinus monophylla)*, California black oak, and curlleaf cercocarpus *(Cercocarpus ledifolius)*. Woodland chaparral is the only chaparral type in which canyon live oak is consistently present; it grows with manzanita, ceanothus, birchleaf cercocarpus, interior live oak, and scrub oak *(11)*.

Throughout California, canyon live oak is an associate in the cypress groves of Santa Cruz cypress *(Cupressus goveniana* var. *abramsiana)*, Tecate cypress *(C. guadalupensis* var. *forbesii)*, Sargent cypress *(C. sargentii)*, and Cuyamaca cypress *(C. arizonica* var. *stephensonii)*. It is associated with singleleaf pinyon in the eastern-southern Sierra Nevada. In the Mojave Desert, canyon live oak is a minor associate of the montane white fir forests *(1)*.

In Arizona, canyon live oak is a minor climax species in the montane Douglas-fir and pinyon forests. It is an understory component in pure stands of Douglas-fir. At lower elevations, it is also a major shrub in oak-chaparral communities, associated with Gambel oak *(Quercus gambelii)*, New Mexico locust *(Robinia neomexicana)*, buckthorn cercocarpus, silktassel bush *(Garrya flavescens)*, Gregg ceanothus *(Ceanothus greggii)*, and manzanita *(17)*.

In Baja California, Mexico, canyon live oak is found in three habitats: in a scrub-chaparral type, as a shrub associated with manzanita and buckwheats *(Eriogonum* spp.); in groves on steep canyon slopes, as a small tree associated with Baja oak *(Quercus peninsularis)*, buckthorn, manzanita, and ceanothus; and at higher elevations, as a small tree in Jeffrey pine forests *(17)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Canyon live oak trees begin to produce flowers at the age of 15 to 20 years. It is monoecious; both male and female flowers are borne on the same tree throughout the crown. The male flowers are in tawny, slender, tomentose catkins 5 to 10 cm (1.95 to 3.90 in) long. The female flowers are solitary or occasionally short, sparsely flowered spikes, tawny with bright red stigmas. The pollen is dispersed by the wind at the time the flowers are receptive. The uniform scattering of male and female flowers throughout the crown is apparently effective in inhibiting selfing. Flowering and pollination occur from May to June, usually later than associated conifers.

Seed Production and Dissemination—The acorns are ellipsoidal, light chestnut brown, 2.5 to 5.1 cm (1 to 2 in) long and 13 to 19 mm (0.5 to 0.75 in) wide. They are enclosed only at the base with a thick, shallow cup covered with golden tomentum. Cleaned seeds vary from 110 to 310/kg (50 to 150/lb).

Acorn crops vary from light to heavy *(4)*. Dry weight yields of fallen acorns in dense stands of canyon live oak range from 10 to 2195 kg/ha (9 to 1,960 lb/acre). A few open-grown trees produce large seed crops, up to 181 kg (400 lb) of acorns per tree *(23)*. Some trees bear acorns every year; the interval between good seed crops varies from 2 to 4 years. In dense stands, trees in sprout clumps usually produce fewer acorns than larger single trees.

The acorns mature in one season and fall to the ground in October. The large, heavy acorns are usually dispersed within a short distance of the tree *(13)*. An occasional acorn, however, may roll a considerable distance down the steep canyon walls of its normal habitat. Animals and birds gathering food disseminate the acorn over wide distances.

Seedling Development—In stands of canyon live oak, seedling regeneration can be very dense and evenly distributed. Seedlings show little seedbed preference, but they do best under an overstory or on the shaded overstory fringe. The best seedbed is moist soil covered with leaf litter. Few uncovered acorns germinate. Germination is hypogeal, and a short, cold stratification pretreatment helps to break dormancy. Germination occurs in early spring, and the percentage of seed germinating is moderate. The juvenile root penetrates moist soil rapidly, and survival is high under the shade of dense stands. Competition from grass can cause a complete failure in dry years.

Early seedling growth is slow, and large numbers of seedlings accumulate in some stands *(7,13)*.

Vegetative Reproduction—Canyon live oak reproduces by sprouts that develop from dormant buds under the bark at the base of trees. Sprouts may form after a minor injury, such as browsing, or when the aerial parts of a tree are destroyed by fire or harvesting *(21)*.

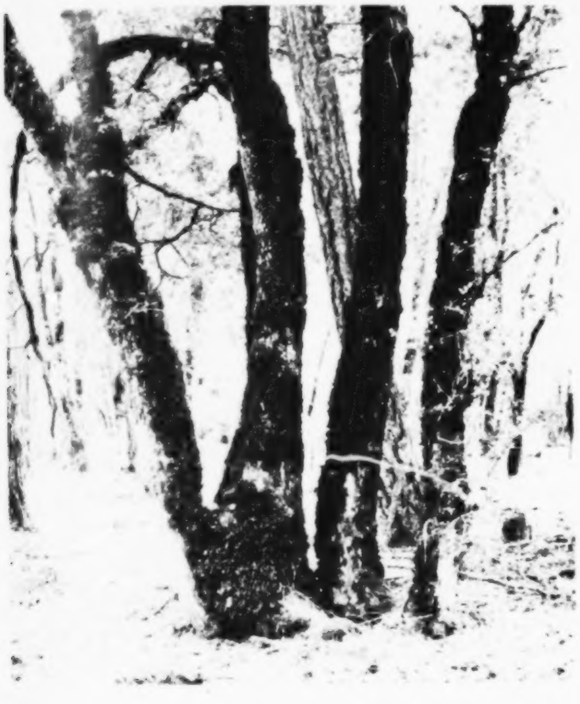

Figure 2—*Clumps of canyon live oak originating from sprouts in a 70-year-old canyon live oak–Douglas-fir stand. (Photo by author)*

Sprouts develop from any size tree or shrub immediately after an injury. Older, less vigorous trees may produce only stool sprouts or none. The size and vigor of the parent tree or shrub determine the early height growth and number of sprouts per clump. Sprout development is greater on larger, more vigorous parent trees. Sprout growth of 0.5 to 1 m (1.6 to 3.3 ft) has been measured the first year. The

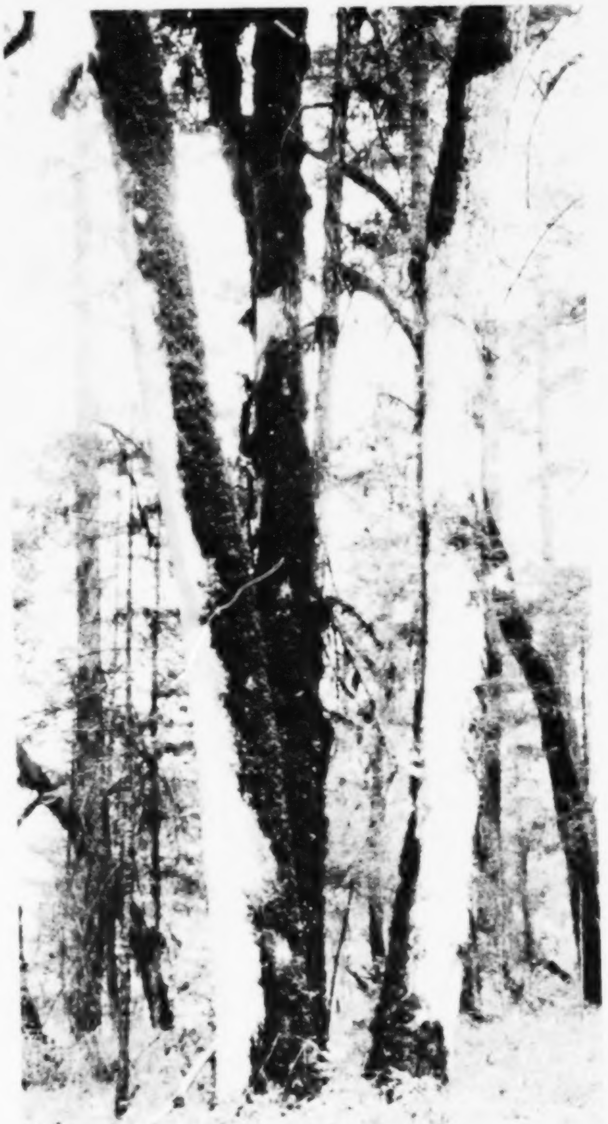

Figure 3—*Large canyon live oak and Douglas-fir in the* Pseudotsuga menziesii–Quercus chrysolepis/Rhus diversiloba *type of the mixed evergreen forests in northern California. (Photo by author)*

number of sprouts per clump is gradually reduced as growth is concentrated on the dominant members. When nearly 100 years old, a parent tree may have three to five stems per clump (fig. 2). Individual stems in these clumps are seldom as large as single trees *(13)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth from sapling stage to maturity is slow. In dense, mature stands where oaks are associated with conifers, heights of canyon live oak range from 18 to 30 m (60 to 100 ft), and trunks are straight and free of branches for 6 to 12 m (20 to 40 ft) (fig. 3). Trees may reach 152 cm (60 in) in d.b.h. *(3)*. In open situations, canyon live oak grows less in height but has a large dome-shaped crown as wide as 38 m (125 ft).

In mature stands of canyon live oak, basal areas reach 125 m^2/ha (545 ft^2/acre); most stems are in the 50- to 70-cm (20- to 28-in) diameter class. The mean volume of sampled stands in California was 105 m^3/ha (1,503 ft^3/acre) with a maximum volume of 289 m^3/ha (4,128 ft^3/acre) *(2)*.

Rooting Habit—Canyon live oak has rapidly growing, deeply penetrating juvenile roots. At maturity in coarse-textured soils, it is deep rooted with a pronounced taproot. In very rocky soils, the roots may be shallow and cover a large area, with occasional large roots extending for some distance near the surface.

Reaction to Competition—Canyon live oak is tolerant of shade and has a higher degree of drought tolerance than associated oaks. In the southern portion of its range, it has the ability to germinate and grow at a slow rate under dense stands of other species. Most stands free of recent major disturbance have trees of all sizes and all ages.

In the Coast Ranges of central California, canyon live oak reproduces under woodland stands of blue oak, valley oak *(Quercus lobata)*, and coast live oak where fire is excluded *(8)*.

In the northern portion of its range, canyon live oak is less tolerant of shade than its associates in the mixed evergreen forests—tanoak, giant chinkapin, and Douglas-fir—and is usually more tolerant than Pacific madrone. Canyon live oak occurs as an early successional shrub or tree on good sites but is soon outgrown by its associates and eliminated from a stand. On drier, more open sites, it persists in the climax forest as a subordinate tree and shrub *(10,16,20)*. Only on very rocky, steep canyon walls does it occur as a dominant in the climax forest.

As sawtimber, canyon live oak is best managed in even-aged stands, mixed with different conifers: ponderosa pine in the northern portion of its range, Digger pine in the central Coast Ranges, and Coulter pine and bigcone Douglas-fir in southern California. Closed canopies should be maintained at all times, because open-grown canyon live oak tend to develop short boles, poor form, and excessive crowns with large branches. Maximum production of biomass for fuelwood can be achieved in pure, even-aged coppice stands.

Damaging Agents—Canyon live oak seedlings and saplings are browsed by deer. In some areas, as many as 40 percent of all seedlings were browsed *(8)*. In most situations, however, growth is not seriously retarded. Young stands of canyon live oak are relatively vulnerable to ground and crown fires. The combustion of ground fuels and brush during light fires singes and kills the crown foliage and burns through the thin, flaky bark. Repeated fires tend to convert canyon live oak trees to shrubs *(18)*. In southern California, crown-sprouting associates—such as coast live oak and bigcone Douglas-fir—remain as trees after repeated fires, whereas canyon live oak becomes a shrub *(14)*.

Little insect damage has been observed on canyon live oak compared with other oaks. Occasional localized damage is caused by California oakworm *(Phryganidia californica)* in wet years; in dry years, the Pacific oak twig girdler *(Agrilus angelicus)* causes some damage. Other insects reported to do minor damage on canyon live oak are Pacific tent caterpillar *(Malacosoma constrictum)*, western tussock moth *(Orgyia vetusta)*, carpenterworm *(Prionoxystus robiniae)*, ribbedcase maker *(Bucculatrix albertiella)*, oak bark beetles *(Pseudopityophthorus* sp.), and a false powderpost beetle *(Melalgus confertus) (3)*.

Acorns are destroyed by the filbert weevil *(Curculio uniformis)* and the filbertworm *(Melissopus latiferreanus) (22)*. Often entire crops are riddled by insects. During some years an entire crop of acorns is used as food by squirrels, deer, and birds.

Numerous pathogens are found on canyon live oak throughout its range, the most serious being various heart rots. Diseases of canyon live oak are relatively unimportant under natural conditions. A rust fungus, *Cronartium quercuum*, and the mistletoe *Phoradendron villosum* subsp. *villosum* cause witches' brooms.

Special Uses

Canyon live oak was one of the woods most commonly used by early California settlers for farm implements, shipbuilding, furniture, and fuel. The common name maul oak came from its use as a splitting maul *(5)*. Canyon live oak has been considered a non-manageable hardwood; however, its high caloric value and rapid sprout growth make it an excellent source of fuelwood. Manufactured into paneling, the wood makes an attractive multicolored interior wall covering.

Open-grown trees with their wide crowns of evergreen leaves make attractive urban trees. The ability of canyon live oak to grow on steep, rocky, moving slopes makes it an excellent stabilizer of soils on steep slopes.

Montane hardwood forests dominated by canyon live oak provide habitat and food for a large variety of wildlife. The acorns are an important source of food for scrub and Steller's jays, acorn woodpecker, band-tailed pigeon, wild turkey, mountain quail, ground squirrel, woodrat, black bear, and mule deer. Deer also use the foliage as food. Many amphibians and reptiles are found in these forests *(12,22)*.

Genetics

Considerable ecological and morphological diversity has been reported for canyon live oak throughout its range. The ecological diversity has not actually been determined; however, its occurrence over a broad range of elevations and geographical, topographical, edaphic, and vegetational conditions indicates considerable ecological variability.

Throughout the Coast Ranges of California, a variety of canyon live oak has been recognized—*Quercus chrysolepis* Liebm. var. *nana* (Jepson) Jepson. Apparently this morphological variety is an ecotypic shrubby form of canyon live oak found in the fire chaparral types. At high elevations, the shrubby forms are hybrids between canyon live oak and huckleberry oak *(Q. vaccinifolia)*.

On the California Channel Islands, canyon live oak hybridizes with the endemic island live oak *(Q. tomentella)*, and in Arizona it hybridizes with Dunn oak *(Q. dunnii) (17)*.

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Quercus coccinea Muenchh.   Scarlet Oak

Fagaceae   Beech family

Paul S. Johnson

Scarlet oak (*Quercus coccinea*), also called black oak, red oak, or Spanish oak, is best known for its brilliant autumn color. It is a large rapid-growing tree of the Eastern United States found on a variety of soils in mixed forests, especially light sandy and gravelly upland ridges and slopes. Best development is in the Ohio River Basin. In commerce, the lumber is mixed with that of other red oaks. Scarlet oak is a popular shade tree and has been widely planted in the United States and Europe.

Habitat

Native Range

Scarlet oak (fig. 1) is found from southwestern Maine west to New York, Ohio, southern Michigan, and Indiana; south to southern Illinois, southeastern Missouri, and central Mississippi; east to southern Alabama and southwestern Georgia; and north along the western edge of the Coastal Plain to Virginia.

Climate

The range of scarlet oak is within the humid region. Average annual precipitation ranges from 760 mm (30 in) along the western edge of the region to 1400 mm (55 in) in the southeast and at the higher elevations. Mean annual temperatures and growing season lengths range from about 10° C (50° F) and 120 days in New England to 18° C (65° F) and 240 days in Alabama, Georgia, and South Carolina. Actual temperatures range from a minimum of -33° C (-28° F) in the north to a maximum near 41° C (105° F) in the south.

Soils and Topography

Scarlet oak is found on a wide variety of soils. The soil groups with which it is most frequently associated in the northern portion of its range include Fragiudalfs, Hapludalfs, and Paleudalfs of the order Alfisols (much of these formerly classified as gray-brown podzolic soils). In the northeastern portion of the species range, the predominant soil group is the Dystrochrept of the order Inceptisols (which includes soils formerly classified as brown podzolic). In the south, the species range lies within the area of soil groups that include Fragiudults, Hapiudults, and Paleudults of the order Ultisols (much of these formerly classified as red-yellow podzolic soils).

The site index of scarlet oak at base age 50 years ranges from 11.3 to 27.7 m (37 to 91 ft) in the Missouri Ozarks (*4,15*). In the southern Appalachians, it regenerates and competes best on middle to upper slopes of southern exposure (*17*). However, site index increases with increasing depth of the A horizon, decreasing amounts of sand in the A horizon, and lower position on the slope. In the northern Appalachians, position on the slope, slope gradient, aspect, and soil depth to bedrock are also important site factors (*4*).

Although its successional position has not been defined, scarlet oak is probably a climax tree on dry soils. Because of its hardiness, it can be planted on a wide variety of soils.

Maximum elevation for scarlet oak is about 1520 m (5,000 ft) in the southern Appalachians; it is common at elevations less than 910 m (3,000 ft).

Associated Forest Cover

Scarlet oak is recognized as an important component of 14 forest cover types in North America (*8*). It is a major component of two variants of Chestnut Oak (Society of American Foresters Type 44). The chestnut oak-scarlet oak variant is found on upper slopes and ridge tops in the central Appalachians; the chestnut oak-black oak-scarlet oak variant is common in the Southeast. It is also a major component of three variants of White Oak-Black Oak-Northern Red Oak (Type 52): black oak-scarlet oak, black oak-scarlet oak-chestnut oak, and scarlet oak-chestnut oak. Nearly pure stands of scarlet oak grow in areas of the Ozark Plateau in Missouri.

Other forest types that include scarlet oak as an associate are Northern Pin Oak (Type 14), Post Oak-Blackjack Oak (Type 40), Black Oak (Type 110), Bear Oak (Type 43), White Oak (Type 53), Shortleaf Pine-Oak (Type 76), Loblolly Pine-Hardwood (Type 82), Pitch Pine (Type 45), Shortleaf Pine (Type 75), Virginia Pine (Type 79), Virginia Pine-Oak (Type 78), and White Pine-Chestnut Oak (Type 51).

Common less important trees and shrubs associated with scarlet oak include flowering dogwood (*Cornus florida*), mountain-laurel (*Kalmia latifolia*), sourwood (*Oxydendrum arboreum*), and vacciniums (*Vaccinium* spp.).

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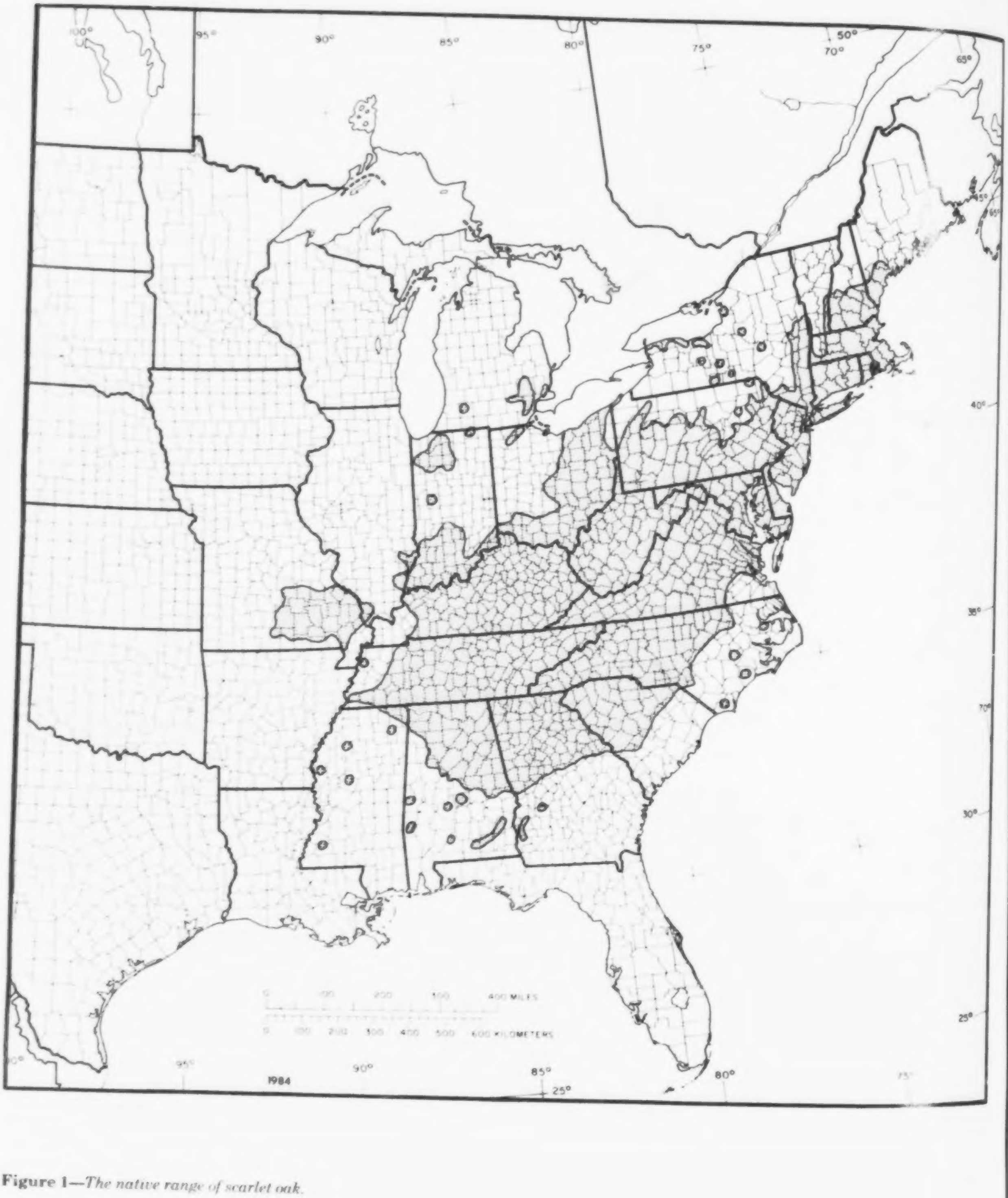
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Figure 1—*The native range of scarlet oak.*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Scarlet oak is monoecious. It flowers in April or May, depending on latitude, elevation, and weather. Two growing seasons are required for the acorns to mature *(20)*.

Seed Production and Dissemination—Minimum seed-bearing age is 20 years, but maximum production does not occur until after 50 years of age. Seed production increases with tree size up to a diameter of 51 cm (20 in), then levels off. On the average, good seed crops occur every 3 to 5 years, although actual seed production may be irregular and unpredictable from year to year. In Missouri, scarlet oak acorn crops tend to be more variable than those of black oak *(Quercus velutina)*, white oak *(Q. alba)*, post oak *(Q. stellata)*, and blackjack oak *(Q. marilandica) (4,5)*.

Maximum annual production of mature scarlet oak acorns in Missouri for a 4-year period was about 25 acorns per square meter (2 or 3/ft^2) of crown area *(18)*. In contrast, maximum annual production of black oak and white oak acorns was 70 to 75/m^2 (about 7/ft^2) during the same period. In the Southeast, scarlet oak acorn production has averaged 14.6 kg/m^2 (3.0 lb/ft^2) of basal area of scarlet red oak trees for a 12-year period *(2)*. This production rate was about 25 percent of northern red oak *(Quercus rubra)* and about 36 percent of white oak during the same period; however, scarlet oak acorn production exceeded that of black oak and chestnut oak *(Q. prinus)*.

More than 80 percent of mature scarlet oak acorns may be destroyed by insects. Most insect damage occurs after acorn fall. The most important insect pests are nut weevils *(Curculio* spp.), moth larvae (Lepidoptera), and cynipid gall wasps (Cynipidae) *(18)*. The proportion of uninfested acorns is usually highest in years of greatest seed production.

Scarlet oak acorns are a choice food for eastern gray squirrels, chipmunks, mice, wild turkey, deer, and birds, especially blue jays and red-headed woodpeckers (4). One-third to one-half of acorn losses have been attributed to removal by birds and squirrels while the acorns were still on the tree.

Seedling Development—A light covering of forest litter is beneficial to the germination of scarlet oak acorns; no litter or a deep litter is less favorable. A moderately open overstory canopy provides a more favorable environment for acorn germination than does a completely closed or very open canopy *(4)*. Germination is hypogeal.

Shoots of scarlet oak seedlings commonly die back and resprout, thus forming seedling sprouts; resprouting occurs from dormant buds at or above the root collar. As a result of recurrent shoot dieback, root systems of scarlet oaks may be many years older than shoots. The potential rate of annual height growth of this reproduction increases with increasing basal diameter of sprouts *(23)*. Young stump sprouts may produce up to three flushes of shoot growth per growing season *(6)*. However, individual flush lengths get progressively shorter as the season progresses. Despite the initial rapid height growth of scarlet oak stump sprouts, a comparison of site index curves for sprouts with conventional curves indicated that the height growth of sprouts falls off rapidly after 20 years *(26)*.

A two-cut shelterwood method has been recommended to regenerate scarlet oaks with the first cut made to provide a favorable germination environment *(4)*. The second cut is made to release the advanced regeneration as soon as sufficient numbers of stems are large enough to successfully compete with the other vegetation that will develop when the remaining overstory is removed *(24)*.

Vegetative Reproduction—Scarlet oak stumps produce sprouts at greater ages and larger sizes than most other oaks *(4)*. They also produce a larger number of sprouts per stump and these sprouts grow faster than those of most associated oaks, hickories *(Carya* spp.), and red maple *(Acer rubrum)* during the first 5 years *(25)*. However, the percent of stumps that sprout decreases from near 100 percent for trees 10 cm (4 in) d.b.h. and smaller to about 18 percent for trees 61 cm (24 in) d.b.h. *(11)*.

In a study of scarlet oak sprouts in the Appalachians, 28 percent had butt rot, and sprouts from large stumps were more subject to butt rot than sprouts from small stumps *(22)*. As the sprouts grow older, the rot spreads and may weaken the trees to a point where they break off during high winds. Because of poor natural pruning, only one-third of scarlet oak crop trees originating from sprouts produce stems with desirable bole quality, even on good sites, i.e., oak site index 23 m (75 ft) *(27)*. However, in coppice stands, thinning sprout clumps to one stem can increase growth and survival of the remaining stem *(14)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Scarlet oak (figs. 2, 3) is a medium-sized tree, normally maturing when 18 to 24

Figure 2—*An excellent group of 54-year-old scarlet oaks in South Carolina.*

m (60 to 80 ft) tall and 61 to 91 cm (24 to 36 in) d.b.h. Maximum size is about 30 m (100 ft) in height and 122 cm (48 in) in d.b.h. The tree grows rapidly and matures early. Economic maturity is reached at 46 to 58 cm (18 to 23 in) d.b.h., depending on vigor class *(4)*.

In diameter growth, scarlet oak ranks ahead or equal to that of associated oaks. Among 11 species compared in pole-size stands in the Central States, average 10-year diameter growth for scarlet oaks was exceeded only by yellow-poplar *(Liriodendron tulipifera)* and black walnut *(Juglans nigra)* *(9)*. However, on poor sites, scarlet oak probably grows more rapidly than any of its associates *(4)*. Yields of fully stocked unthinned oak stands in which scarlet oak is present range at age 80 from about 75.6 m^3/ha (5,400 fbm/acre) for site index 55 to 175.0 m^3/ha (12,500 fbm/acre) for site index 75 *(10)*. Thinning scarlet oak stands can greatly increase growth and quality of individual trees *(7,12)*.

Rooting Habit—Scarlet oak seedlings develop a strong taproot with relatively few lateral roots. Difficulties in transplanting this species may be related to its coarse root system plus its relatively slow rate of root regeneration *(16)*.

Figure 3—*A mature scarlet oak in the Mark Twain National Forest, MO.*

Reaction to Competition—Scarlet oak is classed as very intolerant of shade. Except for reproduction under older stands, it is usually found only as a dominant or codominant *(4)*. Its absence in suppressed or intermediate positions is indicative of its intolerance. It probably maintains its dominance on dry sites because of its rapid growth and drought tolerance, and because of light conditions that are adequate for the establishment and development of reproduction *(4,21)*.

When site index is equal, scarlet oak tends to be better represented in forests with a fire history than in forests with little or no evidence of past burning *(3)*. Its better representation on burned sites may be related to its vigorous sprouting ability after burning, together with the elimination of more fire-sensitive competitors.

Damaging Agents—Because of its thin bark, scarlet oak is very susceptible to fire damage. If not killed outright, the tree is usually injured so that sap or heart rots enter *(4)*. This weakness, coupled with a dry environment, helps explain the high mortality or severe damage to trees even from light ground fires. Nevertheless, basal sprouting from fire-killed scarlet oaks may be prolific.

Heart rots of scarlet oak can enter the bole through branch stubs even at an early age and cause severe damage. Heart rots are especially common in stump sprouts that originate high on the stump *(4)*. In one study, decay in scarlet oak sprouts that originated at or below ground line was only 9 percent, whereas decay in sprouts originating 2.5 cm (1 in) or more above ground was 44 percent *(22)*. The fungus *Stereum gausapatum*, which is transmitted from stump to sprout, was the most common cause of decay.

Scarlet oak is also susceptible to oak wilt (*Ceratocystis fagacearum*). Trees attacked by this fungus may die within a month after the first symptoms appear. This oak is also subject to cankers of *Nectria* spp. and *Strummella coryneoidea*. These diseases are especially severe from Virginia northward *(4)*.

The major insect defoliators in scarlet oak include the oak leaftier (*Croesia semipurpurana*), fall cankerworm (*Alsophila pometaria*), forest tent caterpillar (*Malacosoma disstria*), gypsy moth (*Lymantria dispar*), and orangestriped oakworm (*Anisota senatoria*) *(19)*. Coupled with defoliation by spring frosts, repeated defoliation by these insects either individually or in combination is thought to be the primary cause of "decline" and mortality of scarlet oak and other oaks in the red oak group in Pennsylvania. Similarly, in the Missouri Ozarks, scarlet oak decline has been linked to a complex of factors including insects, disease, drought, and soil-site relations *(13)*.

The walkingstick (*Diapheromera femorata*) may severely defoliate scarlet oak, particularly in the northern portion of the scarlet oak range. The twolined chestnut borer (*Agrilus bilineatus*) is a secondary pest of scarlet and other oaks following drought, fire, frost damage, or defoliation by other insects. Larvae of carpenterworms (*Prionoxystus* sp.) can damage scarlet oak by tunneling into heartwood and sapwood. They prefer open grown trees or trees growing on poor sites. Ambrosia beetles (*Platypus* sp. and *Xyleborus* sp.) and the oak timberworm (*Arrhenodes minutus*) can invade and damage freshly cut or wounded trees *(4)*. The red oak borer (*Enaphalodes rufulus*) breeds in trunks of living trees greater than 5 cm (2 in) d.b.h. Larvae bore into phloem and cause serious defect and degrade; ants and fungi may then enter wounds and cause further injury *(1)*. The black carpenter ant (*Camponotus pennsylvanicus*) sometimes nests in standing trees. Ants may enter the tree through stem cracks, scars, and holes and may extend their galleries into sound wood *(1)*. The gouty oak gall wasp (*Callirhytis quercuepunctata*) can produce galls on twigs and smaller limbs of scarlet oak, and heavy infestations may kill the entire tree. Also, the large oak-apple gall wasp (*Amphibolips confluenta*) may cause gall on the leaves or leaf petioles of scarlet oak *(1)*.

Special Uses

In addition to its value as a timber and wildlife species, scarlet oak is widely planted as an ornamental. Its brilliant red autumn color, open crown texture, and rapid growth make it a desirable tree for yard, street, and park.

Genetics

Scarlet oak hybridizes with black oak (*Quercus velutina*), producing *Q.* × *fontana* Laughlin, and with bear oak (*Quercus ilicifolia*), producing *Q.* × *robbinsii* Trel.; it also hybridizes with pin oak (*Q. palustris*).

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Quercus douglasii Hook. & Arn. **Blue Oak**

Fagaceae **Beech family**

Philip M. McDonald

Blue oak (*Quercus douglasii*), named for its blue-green foliage, is also known as iron oak, mountain white oak, or mountain oak. This species is currently underutilized and unmanaged. Silvicultural systems for it are unknown. Blue oak is often found in extensive open stands in the interior foothills where it grows slowly on dry, loamy, gravelly, or rocky soils. It is used locally for fenceposts and fuelwood, and the acorns are an important food for several kinds of wildlife.

Habitat

Natural Range

Blue oak (figs. 1, 2), a California endemic, has a north–south range of about 740 km (460 mi). Its distribution, in general, surrounds California's Central Valley. Northern limits are Montgomery Creek in Shasta County and southern limits are in the Liebre Mountains of Los Angeles County and the Santa Ynez Valley of Santa Barbara County. Blue oaks are scattered over the landscape above Mission Santa Barbara less than 5 km (3 mi) from the Pacific Coast, and on Santa Cruz and Santa Catalina Islands (*11*).

Climate

Hot dry summers and cool wet winters typify the climate where blue oaks are found. The mean maximum July temperature averages 32° C (90° F) and the mean January minimum –1° C (30° F). Temperatures for stands outside the main distribution, especially at higher and lower elevations and on the border of the Mojave Desert, vary much more. Mean July maximum temperatures range between 21° and 38° C (70° and 100° F) and mean January minimums from -12° to 2° C (10° to 35° F). The frost-free growing season varies from 150 to 300 days.

Annual precipitation averages 510 to 1020 mm (20 to 40 in) within the main distribution of blue oak. At extremes of the natural range, 1520 mm (60 in) in Shasta County and 250 mm (10 in) in Kern County bracket the annual fall of moisture. Throughout, most of the precipitation is rain, although snow occasionally blankets the land. Most precipitation (60 to 90 percent) occurs between November 1 and April 30.

Soils and Topography

Soils from a variety of parent materials support blue oak. They are characteristically shallow, skeletal, infertile, thermic, and moderately to excessively well drained. Textures range from gravelly loam through stony clay loam. Soils with extensive rock fragments in the profile commonly support this oak; as much as 50 percent of the surface area of a soil may be covered with stones or rock outcrops. Blue oaks are found on soils with depths of 51 to 102 cm (20 to 40 in), but scattered trees grow on soils ranging from 30 to 51 cm (12 to 20 in). Soil orders for blue oak are Alfisols and Inceptisols, occasionally Mollisols. More than 40 soil series in California have been identified by the California Cooperative Soil–Vegetation Survey and the National Cooperative Soil Survey as supporting blue oak. The principal California mountain ranges and soil series are as follows:

Mountain Range and Subrange	**Soil Series**
Coast	
North Coast	Hulls, Laughlin, Sehorn
Central Coast	Gazos, Hambright, Henneke, Hillgate, Los Osos, Millsap, Millsholm, Sobrante
Central Valley floor	Arbuckle
Cascade	
Southern	Guenoc, Toomes, Gaviota, Iron Mountain, Stover
Sierra Nevada	Ahwahnee, Auberry, Auburn, Blasingame, Coarsegold, Guenoc, Inks, Sierra, Millerton, Stover, Toomes, Trabuco
Transverse and Peninsular	Gilroy, Havala, Perkins, Tehachapi

The one characteristic found most often in soils supporting blue oak is high base saturation. Values of at least 50 percent or even 90 to 100 percent are common (*19*). Soils within blue oak's natural range that do not support it are generally drained poorly or are of heavy clay texture, often with a hardpan near the soil surface. Deep fertile soils are seldom clothed with blue oak because this species is not competitive with the inherently taller conifers or the better adapted interior live oak (*Quercus wislizenii*) and California black oak (*Q. kelloggii*).

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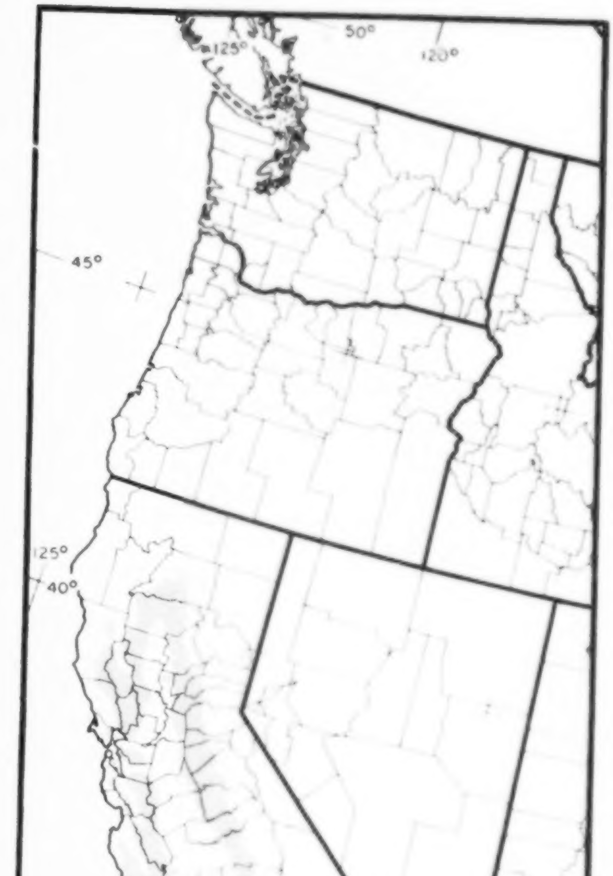

Figure 1—*The native range of blue oak.*

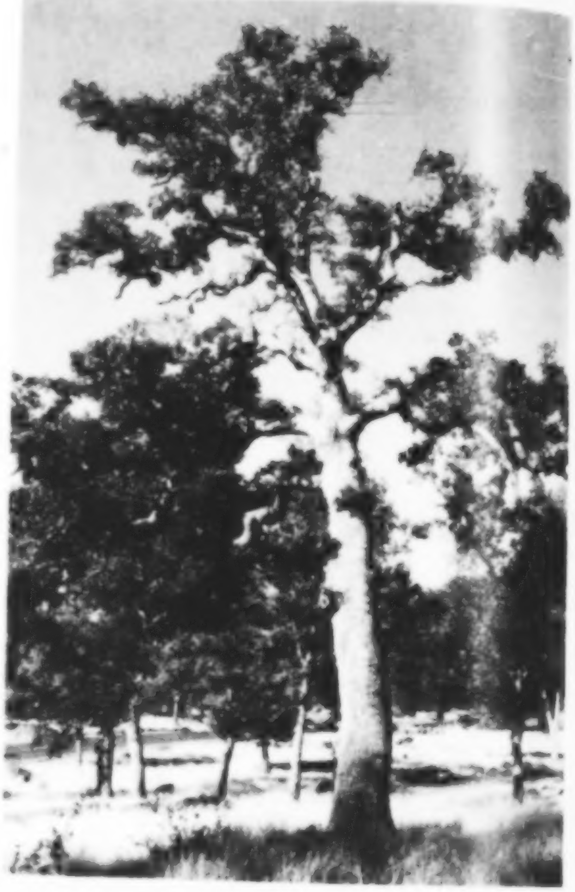

Figure 2—*A white-barked blue oak in Shasta County, CA, 12 m tall and 81 cm in d.b.h.*

Blue oak grows within a fairly wide elevational range—from the valley floor in the north to the midslopes of Mount Pinos in the south. Corresponding elevational limits are 50 to 1800 m (165 to 5,900 ft). At the north end of the Sacramento Valley and in the foothills of the southern Cascade and Klamath Mountains, the general elevational range of blue oak is 152 to 610 m (500 to 2,000 ft). The species is common between 76 and 915 m (250 and 3,000 ft) in the central Coast Range, and between 168 and 1370 m (550 and 4,500 ft) in the Transverse and Peninsular Ranges. On west slopes of the Sierra Nevada, the species is abundant in the foothills at an elevational range of 152 to 915 m (500 to 3,000 ft) (35).

Associated Forest Cover

Blue oak is the principal component of the forest cover type Blue Oak–Digger Pine (Society of American Foresters Type 250) *(25)*. In general, it is neighbor to California Black Oak (Type 246) and Pacific Ponderosa Pine (Type 245) at higher elevations and to the annual grass savannah at lower elevations. In the northern Coast Range, and in the foothills of the Klamath Mountains, Oregon White Oak (Type 233) often abuts Blue Oak–Digger Pine. In portions of its range, the upper elevational border of blue oak often grades into more dense stands of interior live oak and chaparral. Similarly at lower elevations it blends into more open stands of valley oak *(Quercus lobata)*. Throughout, dense stands and scattered patches of chaparral are often present. A grassy understory almost always can be found beneath blue oak trees. Stands of scrubby oaks sometimes bridge the gap between oak trees and woody shrubs in parts of the blue oak range. For most of the range, blue oak should be regarded as a component of a mosaic that includes savannah, chaparral, other deciduous and evergreen oaks, and at least one common conifer.

The paleobotanic record of blue oak shows a Miocene progenitor, *Quercus douglasoides*, which apparently inhabited a wider natural distribution than its modern counterpart. In the next epoch, the Pliocene, blue oak's fossilized equivalent, *Q. orindensis*, grew in a habitat of dry open slopes bordering valleys. It was associated with several chaparral species, a few elements of the broad-sclerophyll forest, several riparian species, and an occasional redwood and fir *(7)*.

The California oak woodland, in general, is recognized as climax, but the successional status of blue oak is not clear. A substantiating tenet of climax is that the same vegetation returns after each gross disturbance. Fire and grazing are, and have been, chronic to the point that the present stands are still recovering from them. That the oak woodland exists after all this disturbance, and that its boundaries have remained rather constant, support the designation of climax *(10)*.

The most common tree associate of blue oak is Digger pine *(Pinus sabiniana)*; however, blue oak extends farther into valleys, but not as far into montane regions as the pine. Blue oak is usually the majority species, Digger pine inevitably the taller. Other occasional conifer associates are ponderosa pine *(Pinus ponderosa* var. *ponderosa)*, knobcone pine *(P. attenuata)* and, in a more limited area, Coulter pine *(P. coulteri)*. California juniper *(Juniperus californica)* and singleleaf pinyon *(Pinus monophylla)* are infrequent associates in the Tehachapi and Piute Ranges of southern California.

Interior live oak and valley oak are the most common hardwood associates of blue oak. Others are California black oak, coast live oak *(Quercus agrifolia)*, Oregon white oak *(Q. garryana)*, toyon *(Heteromeles arbutifolia)*, California redbud *(Cercis occidentalis)*, and California buckeye *(Aesculus californica)*.

Shrub associates of blue oak in its main distribution are neither abundant nor diverse. Principal shrub associates are: common manzanita *(Arctostaphylos manzanita)*, mariposa manzanita *(A. mariposa)*, whiteleaf manzanita *(A. viscida)*, buckbrush *(Ceanothus cuneatus)*, poison-oak *(Toxicodendron diversilobum)*, yerba santa *(Eriodictyon californicum)*, foothill gooseberry *(Ribes quercetorum)*, and chaparral coffeeberry *(Rhamnus californica tomentella)*.

Grasses are particularly abundant in the natural range of blue oak. Originally they were of the bunchgrass type, *Stipa* (needlegrass) being the most common genus. Introduced annual grasses, especially the wild oats *(Avena fatua* and *A. barbata)* have replaced the perennial grasses almost completely. Other annual grasses common beneath blue oak are members of the genera *Bromus* and *Hordeum*.

Blue oak adapts well to harsh environments, especially aridity. In mid-August of a dry year, valley oak and coast live oak on alluvial soils indicated a minimum (predawn) moisture stress of only 2.03 to 5.07 bars (2 to 5 atmospheres). Nearby blue oaks on an upland soil showed 27.36 bars (27 atmospheres) of stress *(10)*. Blue oak sheds its leaves when stress becomes prohibitive, thus conserving moisture. This ability to withstand more severe moisture stress than its associates contributes to the pattern of blue oak distribution over the landscape.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Blue oak is monoecious; its flowers are unisexual. Staminate flowers are borne in slender drooping catkins, one or more from lower axils of leaves of the previous year. Pistillate flowers are greenish-yellow and originate from leaf axils of the current year *(26)*. Blue oak flowers from late March to mid-May, depending on elevation, aspect, climate, and reproductive capability of individual trees. In general, trees at lower elevations and on warmer aspects bloom first. On long continuous hillsides, however, blooming is first on midslopes—above areas of cold air ponding and below ridgetops.

Acorns mature in one growing season. When about half size, the cup covers about half the acorn, but at maturity the cup encapsulates only 10 to 20 percent of it. The elliptical, often tear-shaped acorns form singly or in clusters of two, rarely three, and are variable in size and shape. Fully developed acorns range from 2.5 to 4.0 cm (1.0 to 1.6 in) in length and from 12 to 21 mm (0.5 to 0.8 in) in diameter. Acorns range in color from light green during development to yellowish-green in early September, to medium-dark brown at maturity.

Seed Production and Dissemination—Abundant seed crops are produced every 2 to 3 years, with bumper crops every 5 to 8 years *(26)*. In other years at least a few trees are fruitful.

Aborted acorns begin falling in July and are mostly gone from the trees by late August. Insect-infested acorns fall in late August to mid-September, usually preceding the fall of mature acorns. Most sound acorns fall between mid-September and the end of October. They average 45/kg (100 seed/lb) and range from 25 to 82/kg (55 to 180/lb).

Seed crops vary in size. On one area the acorn crop ranged from 0.14 to 25.31 kg (0.31 to 55.81 lb) per tree per year; on another an average-sized blue oak produced 215 acorns per square meter (20/ft^2) of collecting ground during a good seed year or 73 kg (160 lb) of acorns per tree.

Data relating acorn production to tree size are scanty. A single blue oak in Shasta County, 34 cm (13.5 in) in d.b.h., 11.6 m (38 ft) tall, and 4.3 m (14.0 ft) in crown width, produced an estimated 3,750 acorns during an especially productive year. At least some roots of this tree, however, extended beneath a well-watered lawn. An examination in December beneath this and nearby trees showed that all developed acorns had been consumed or carried away.

Two insects produce larvae that destroy many acorns before maturity. Developing acorns are attacked by the filbert weevil *(Curculio uniformis)* and by the filbert worm *(Melissopus latiferreanus)*. Larvae of the filbert weevil are short, fat, glistening, white, legless worms. They mine inside the acorn and destroy its contents. Larvae of the filbertworm often hollow out the acorn, leaving behind a mass of webbing and frass *(5)*.

Acorns are eaten by at least a dozen species of songbirds, several upland gamebirds, several small mammals (mostly rodents), and a few large mammals. Although many acorns are consumed, some are dropped or lost—aiding in the dissemination of the oak. Principal consumers of blue oak acorns include the acorn woodpecker, scrub jay, band-tailed pigeon, California quail, western gray squirrel, and the California ground squirrel *(21)*. The acorns are a valuable foodstuff, along with green and dead leaves, for deer, cattle, sheep, and hogs *(8)*.

For the acorn woodpecker, acorns are the "staff of life." Those from blue oak enable this bird to widen its natural range to include extensive areas of the Central Valley and surrounding foothills *(30)*. For band-tailed pigeons, crop and stomach analyses indicated blue oak acorns constituted 5.8 percent of total food volume in November *(32)*.

Western gray squirrels were collected below the chaparral zone in Mendocino County where blue oak was the majority species. Acorns amounted to 38 percent of total yearly diet and were consumed each month from September through April *(34)*. In Madera County, CA, ground squirrels consume blue oak acorns each month of the year. Acorns constitute 1 to 56 percent of this rodent's total diet each month *(31)*. Acorns of blue oak are critical to migrating deer who leave a dried-up summer range in the Sierra Nevada and travel to a winter range at lower elevations. Acorns picked up en route provide energy and protein not only for travel, but also help to ensure healthy animals during the breeding season.

Seedling Development—On the basis of frequency and magnitude of seed crops, blue oak has the potential to reproduce adequately from seed. During the last 50 to 80 years, however, it appears to have reproduced poorly. In Tulare County, only 7 percent of 405 trees, as determined from increment cores, were less than 60 years old *(22)*. In southern Shasta County, on a green fuelbreak 30.5 m (100 ft) wide along a highway, only blue oaks remained in some places, with several grasses and a few woody shrubs below. The oaks were evenly spaced and formed a parklike stand which might be expected to reproduce well, but when 0.8 km (0.5 mi) of the fuelbreak was examined, only eight seedlings were found *(24)*.

Blue oak seedlings were not always scarce. In 1908, Sudworth *(35)* reported seedlings scarce on cultivated or grazed ground but "rather abundant elsewhere." Cooper *(6)* noted that "typical stands of young *Quercus douglasii* have been seen where it is certain that chaparral was formerly in control." Griffin *(10)* also noted that "the oak produced well at an earlier period" (before 1930) in the Santa Lucia Range. Heavy consumption of acorns and damage to seedlings by deer, cattle, sheep, hogs, insects, and rodents, and especially by ground squirrels and pocket gophers, are possible reasons why blue oaks have not reproduced adequately during the past 60 to 80 years. Environmental and chemical inhibition of acorn germination as a result of introduced annual grasses is another possible reason. Single environmental and habitat factors probably are not adequate to explain the paucity of blue oak reproduction *(1,23)*.

For successful germination, the seeds must be covered. Thick leaf litter or loose mineral soil facilitates germination and early seedling survival. Acorns will germinate on the soil surface in the rare event that temperatures remain low and moisture adequate.

Acorns of the white oak group do not require stratification for germination. Blue oak acorns can, and do, germinate within a month of seedfall. Most, however, germinate early in the spring when warmer temperatures prevail. Germination is hypogeal. Light, moisture, temperature, and the depth of soil or litter covering the acorns probably affect the timing of germination. Germinative capacity from a limited number of tests was 70 to 72 percent after 30 days *(26)*.

Early growth of blue oak seedlings is poorly documented. One investigator seeded 25 acorns in a granitic soil in November and dug them up in March. Root length ranged from 31 to 68 cm (12 to 27 in) and averaged 49 cm (19 in) *(9)*. After 1 year, blue oak seedlings on a gravelly loam soil in Shasta County averaged about 10 cm (4 in) above ground and 20 cm (8 in) below. A 3-year-old seedling growing in partial shade showed about 18 cm (7 in) of shoots and 28 cm (11 in) of roots. Nearby, a 5-year-old seedling was 18 cm (7 in) tall with a single taproot 66 cm (26 in) long. All eight seedlings in an area cut about 10 years ago were less than 46 cm (18 in) tall *(24)*. All were browsed and most had died back to the root crown and resprouted at least once, often with several stems. This evidence, although limited, suggests that the annual growth rate of blue oak seedlings is probably slow.

Vegetative Reproduction—Two types of sprouts are found on blue oak stumps. Some form at the root collar and are root crown sprouts, and others form on the side or top of cut and burned stumps and are stool sprouts.

Blue oak produces sprouts after cutting or fire, but in general is regarded as a weak sprouter. Whether this characteristic results from lack of early sprout vigor or from lack of eventual survival is not clear. Nearly 40 blue oak stumps in a southern Shasta County fuelbreak were examined, and the average number of root crown sprouts per clump was recorded. Positions of sprouts on stumps, and stump diameters also were noted. Stump heights averaged 13 cm (5 in) *(24)*. The trees had been cut about 10 years before the stumps were examined. Presumably most of the sprouts began growing soon after, but others could have originated later, and a few obviously were recent. Sprouts, therefore, were assumed to be as old as 10 years.

Number of root crown sprouts related weakly to stump diameter. The number of sprouts per stump increased curvilinearly from about 12 sprouts on 2-cm (1-in) diameter stumps to 27 sprouts on 15-cm (6-in) diameter stumps. Larger stumps, at least up to 22 cm (9 in) in diameter, produced a decreasing number of sprouts. Two stumps larger than 40 cm (16 in) in diameter showed no evidence of sprouting *(24)*. In the inner Coast Range of central California, blue oak produced fewer sprouts than associated oaks and no sprouts on stumps larger than 52 cm (21 in) *(18)*.

When height of sprouts was compared with stump diameter, no relationship was discernible. Much variation was present. Some sprout clumps looked sickly, others thrifty, still others were browsed or infested with galls, while others were free of such maladies. Some sprouts had died back for part of their length and others were dead.

Stool sprouts develop on high stumps, large old stumps, and stumps with debris piled around them. For stumps cut 13 cm (5 in) above ground, only those larger than 20 cm (8 in) in diameter produced stool sprouts. Three 20-cm (8-in) diameter stumps produced mostly stool sprouts and a few root crown sprouts. Another 20-cm (8-in) stump yielded 70 stool sprouts and a 30-cm (12-in) stump produced 12 stool sprouts *(24)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Throughout the range of blue oak, about 90 percent of trees in natural stands are single stems. Some of these may fork just above groundline, but each originates as a single entity. These trees probably grew from acorns. Of the remaining 10 percent, where two or three stems are growing close together, origin could be from closely spaced acorns or from sprouts.

Tree growth is a function of many variables, especially site quality, topography, and stand density. Tree height-diameter site index curves are available *(33)*. Taller blue oak trees frequently grow on deeper soils, near bases of hillsides, or close to ephemeral streams in canyons and draws. In Shasta County, CA, for example, two blue oaks 56 cm (22 in) in d.b.h. were located about 35 m (115 ft) apart. One was growing on an alluvial flat near a permanent stream, the other on an old terrace about 8 m (26 ft) above

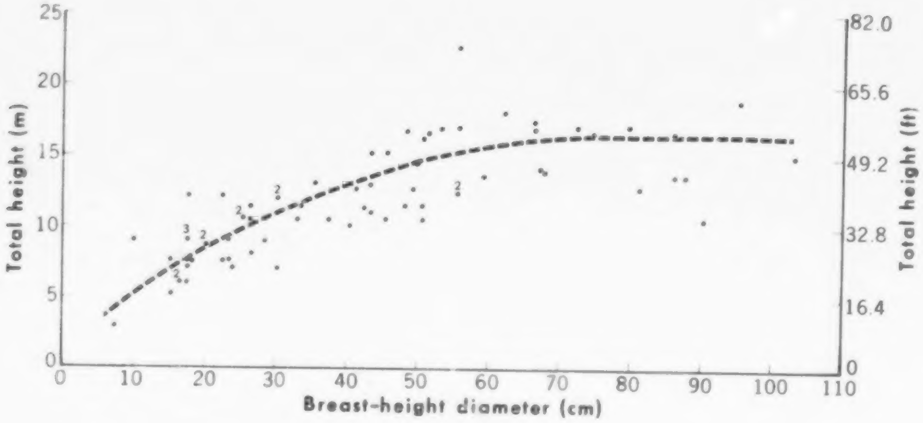

Figure 3—*Diameter-height relationship of dominant blue oaks in natural stands in northern and central California.*

the flat. The two trees differed in height by 10 m (34 ft) *(24)*.

Stand density varies widely from a few trees scattered throughout the savannah to fairly dense stands in the woodland. In the latter, stand density of blue oak can reach more than 1,000 trees per hectare (405/acre) *(10)*. Some stands are made up of trees evenly spaced over the landscape that are remarkably similar in height, diameter, and form. Other stands vary widely, with tree diameters ranging from 8 to 76 cm (3 to 30 in), and with form varying between stunted and crooked stems to those that are straight and tall. Loose groups also are formed. Sometimes a group will consist of trees of a single size class; at other times the group will include trees of several size classes.

Data that quantify tree growth are scarce. Studies in Nevada, Placer, and Shasta Counties show that height growth in general is slow *(24)*. After trees reach 65 cm (26 in) in d.b.h., height growth is extremely slow, or ceases (fig. 3). Blue oak seldom exceeds 125 cm (49 in) in d.b.h. or 25 m (82 ft) in height. A champion blue oak, found in Alameda County, measured 196 cm (77 in) in d.b.h., 28.7 m (94 ft) in height, and had a crown spread of 14.6 m (48 ft) *(27)*.

Diameter-age data also are scanty. Blue oak stands in Tulare County ranged in age from 30 to over 300 years. Regression analyses *(22)* indicated a broad range of age, as determined at 60 cm (24 in) above mean groundline, for a given d.b.h.

D.b.h.		Predicted age	Age range
cm	*in*	*yr*	*yr*
12	5	81	40 to 115
25	10	109	80 to 120
35	14	131	85 to 135

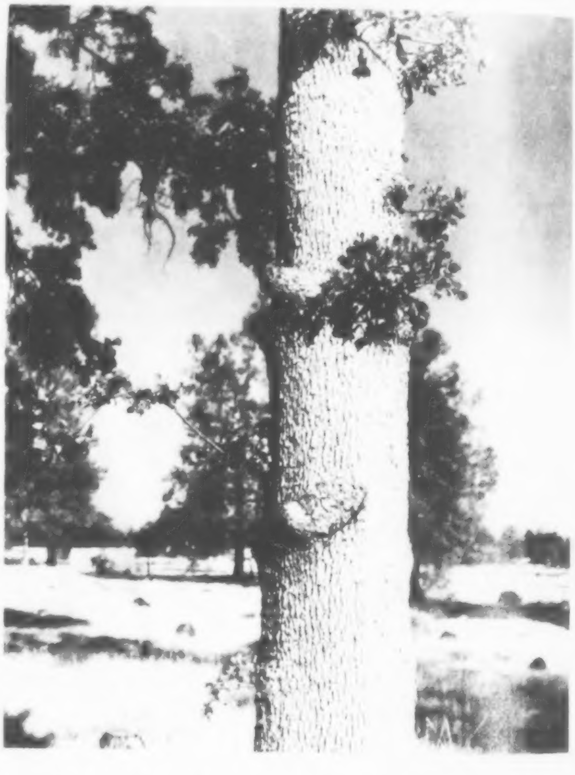

Figure 4—*Epicormic branching on an older blue oak in Shasta County, CA.*

On good sites in Nevada *(36)* and Shasta Counties *(24)*, this relationship proved to be linear for trees up to about 65 cm (26 in) in d.b.h. Trees 20 cm (8 in) in d.b.h. were 40 years old, those 40 cm (16 in) were 82 years old, and trees 60 cm (24 in) in d.b.h. averaged about 125 years. On poorer sites, trees 36 to 51 cm (14 to 20 in) in d.b.h. were from 175 to 280 years old. A large tree in Sequoia National Park was 390 years old *(22)*. The species is believed to live even longer.

Yield information is restricted to volume and weight tables for blue oak in California's central coastal counties *(28)*. Selected gross volumes are as follows:

D.b.h.		Height		Volume	
cm	*in*	*m*	*ft*	m^3	ft^3
10	4	6	20	0.02	0.7
20	8	10	33	0.18	6.4
30	12	10	33	0.47	16.6
40	16	12	39	1.14	40.3
50	20	12	39	1.92	67.8

Epicormic branching is common in blue oaks of all ages (fig. 4). It is greatest on injured trees, recently released trees, and trees bordering openings. In present hardwood log grading rules, it constitutes a degrade. Blue oaks in irrigated lawns and flowerbeds produce many short, weak epicormic branches which, if removed, are replaced every year.

Rooting Habit—The warm dry soils typical of the blue oak habitat mandate that seedling and tree roots grow rapidly downward and stay in a zone of adequate moisture. This suggests a taproot system with one or more deep-growing members. The taproot system begins early in the life of the seedling. Acorns germinate early, before those of other oak associates, and roots grow downward in spite of low temperatures. Most available energy is channeled to development of deep roots, before shoots emerge, and continues after shoot growth begins. The ratio of leaf area to root weight is small. About 73 percent of blue oak's dry weight is allocated to below-ground material the first growing season *(20)*. A study in Placer County, CA, showed that roots from a blue oak 7 cm (3 in) in d.b.h. extended 13 m (42 ft) to groundwater; those of three trees 10 cm (4 in) in d.b.h. penetrated to 20 m (67 ft); and those of an oak 18 cm (7 in) in d.b.h. extended to 24 m (80 ft) *(17)*.

Reaction to Competition—Rarely is blue oak found in an understory. Even when growing in mixed-size groups, the smaller trees are positioned to receive considerable overhead light. The species appears to be adapted to long periods of direct sunlight and can most accurately be classed as intolerant of shade.

Damaging Agents—The bark of blue oak is thin, relative to other oak species, and with age becomes deeply fissured and flaky. It catches fire easily, burns well, and does not provide much protection from fire *(29)*. Leaves on part of the crown, however, can be killed by ground fire one year and replaced the next, with no apparent ill effect to the tree. The species, therefore, is probably better adapted to withstand the quick heat from a grassland fire than to tolerate the more sustained heat from burning chaparral.

Animal damage to blue oak is mostly from loss of foliage by deer, cattle, and other browsers, and from root injury by pocket gophers. Seedlings are particularly vulnerable to both browsers and pocket gophers.

Little has been written about diseases of blue oak, but several are prevalent. Probably the most severe are those that damage the heartwood of the trunk and large limbs. *Inonotus dryophilus* is one of these, causing a white pocket rot in the heartwood of living oaks. The sulphur conk, *Laetiporus sulphureus*, causes a brown cubical rot also of the heartwood of living oaks. The hedgehog fungus (*Hydnum erinaceum*) and the artist's fungus (*Ganoderma applanatum*) are also capable of destroying the heartwood of living oaks.

A disease of blue oak roots that sometimes extends a short distance up the bole is the shoestring fungus rot, *Armillaria mellea*. This fungus gradually weakens trees at the base until they fall. A white root rot caused by *Inonotus dryadeus* also has been reported on blue oak.

Several fungi attack dead sapwood, particularly if the tree is on the ground and in the shade. Two common sapwood decomposers are *Polyporus versicolor* and *Stereum hirsutum*.

A number of diseases attack leaves of blue oak, but most have not been identified. Powdery mildews, especially *Sphaerotheca lanestris* and *Microsphaera alni*, are common. An unknown disease of blue oaks growing in well-watered lawns kills nearly every leaf on the tree in midsummer. The leaves turn brown and persist until the usual time of leaf fall. Normal leaf development takes place the next spring.

True mistletoe (*Phoradendron villosum* subsp. *villosum*) often infects older open-grown blue oaks. Its effect on them is undetermined although the pest must cost its host a certain amount of growth increment.

A large number of insects infest blue oak. One study recorded 38 species of insects in 21 families inhabiting blue oak *(4)*. Two additional insects, a leaf skeletonizer and a wood borer, are recorded in another study *(14)*. No part of the tree is spared. Sucking and chewing insects attack the twigs and leaves, boring insects infest the roots, trunk, and limbs, and other insects ruin twigs and acorns.

Many of the insects are found in low numbers, but when epidemics occur, damage can be severe. A local but intensive epidemic of the fruit-tree leafroller *(Archips argyrospila)*, for example, was noted in Contra Costa County in the early 1970's *(3)*. Blue oaks were badly defoliated by this insect in June; by mid-July a second crop of leaves had taken their place.

More than 40 species of cynipid wasps form galls on blue oak *(38)*. Galls range from small to large, dull to brightly colored, round to oblong, and smooth to spiny. They were found on every part of the tree: the roots, catkins, buds, acorns, stems, and leaves. Of those on stems and leaves, many are firmly attached; others eventually fall to the ground. Two of the most interesting are formed by the spined turban gall wasp *(Antron douglasii)* and jumping oak gall wasp *(Neuoterus saltatorius)*. The turban gall wasp creates from one to four bright purplish-pink galls on the underside of a leaf. The adult jumping oak gall wasp stings the underside of mature blue oak leaves and then lays its eggs inside the leaf. Larvae emerge in July and August and form a light-tan gall less than 0.02 cm (0.06 in) in diameter. These galls fall to the ground about mid-August, often in large numbers, the movement of the larvae causing the ground to seemingly come alive. Possibly the jumping around is an attempt by the larvae within to find cracks and crevices in which to hide, and thereby escape from enemies and bad weather.

Special Uses

Although strong, hard, and heavy, the wood of this oak currently has little or no commercial use, not so much because of its qualities, but because of the short stature and poor form of the tree. Products have been limited to fenceposts and fuelwood, with the latter use increasing greatly in recent years.

Throughout the range of blue oak, especially on its margins and in the Coast Ranges, woody shrubs have been eliminated to encourage forage for livestock, leaving the blue oaks and valley oaks. In other areas, oaks have been reduced greatly or eliminated and a savannah formed with the intent of producing more forage for livestock. When many trees are removed, large increases in forage occur *(15,16)*. When blue oak density is low or moderate, however, the grass seems to be taller, has more nutrients, produces more biomass, grows earlier, and stays greener longer in the growing season under oaks *(12,13)*. Furthermore, living oak roots hold the soil in place on steep slopes and reduce the incidence of mass movement downslope into permanent and ephemeral streams. Elimination of the oaks, therefore, could be a dubious practice.

Blue oak has been used for decoration: large branches hollowed out by heart rot are sawn into sections, cleaned, coated with resin and hardener, and filled with dried seedstalks, for use as wall hangings and table centerpieces.

Blue oak acorns were a favored food of California Indians. On a scale of 1 (preferred) to 3 (undesirable) they rated blue oak acorns 1.5 *(2)*. The acorns average about 4,994 calories per kilogram (2,265/lb) and are a potential source of human food.

Genetics

Blue oak hybridizes with its white oak associates, particularly valley oak, Oregon white oak, California scrub oak *(Q. dumosa)*, and turbinella oak. In most instances the natural hybrids formed by these crosses are fertile and cytologically normal.

The binomial for *Quercus douglasii* × *turbinella* is *Quercus* × *alvordiana* Eastw. and the common name is Alvord oak *(37)*. The Alvord oak is distributed widely from Monterey County southward into the Tehachapi Mountains and is the dominant oak in some foothill woodlands instead of blue oak *(11)*.

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Quercus falcata Michx. Southern Red Oak

Fagaceae **Beech family**

Quercus falcata Michx. var. *falcata* Southern Red Oak (typical)

Roger P. Belanger

Quercus falcata var. *pagodifolia* Ell. Cherrybark Oak

R. M. Krinard

Southern red oak (*Quercus falcata*) has been divided into two varieties, the typical southern red oak (*Q. falcata* var. *falcata*) and cherrybark oak (*Q. falcata* var. *pagodifolia*). There are enough differences between the two to warrant separate discussions here.

SOUTHERN RED OAK

Southern red oak (*Quercus falcata* var. *falcata*), also called Spanish oak, water oak, or red oak, is one of the more common upland southern oaks. This medium-size tree is moderately fast growing on dry, sandy, or clay loams in mixed forests. It is also often found growing as a street or lawn tree. The hard strong wood is coarse grained and used for general construction, furniture, and fuel. Wildlife depend upon the acorns as food.

Habitat

Native Range

Southern red oak (figs. 1, 2) extends from Long Island, NY, southward in New Jersey to northern Florida; west across the Gulf States to the valley of the Brazos River in Texas; north in eastern Oklahoma, Arkansas, southern Missouri, southern Illinois and Ohio, and western West Virginia. It is comparatively rare in the North Atlantic States where it grows only near the coast. In the South Atlantic States its primary habitat is the Piedmont; it is less frequent in the Coastal Plain and is rare in the bottom lands of the Mississippi Delta *(8)*.

Climate

Southern red oak grows where the climate is humid and temperate, characterized by hot summers, mild and short winters, and no distinct dry season. Average annual precipitation is between 1020 and 1270 mm (40 and 50 in), half of which occurs during the April to September growing season. Throughout the major part of its range, the average annual temperature is between 16° and 21° C (60° and 70° F), with daily extremes near -18° C (0° F) to about 38° C (100° F). At the northern extreme of its range the average annual temperature is between 10° and 15° C (50° and 60° F), with extremes of -23° to 38° C (- 10° to 100° F).

Soils and Topography

Southern red oak is characteristically an upland tree, growing on dry, sandy, clay soils *(1)*. It is also found widely on sandy loam, sandy clay loam, and silty clay loam soils. Occasionally it grows along streams in fertile bottoms and here reaches its largest size. Overall, southern red oak is most commonly found growing on soils in the orders Ultisols and Alfisols.

Throughout its range, southern red oak is most frequently found at elevations up to 610 m (2,000 ft) above sea level in both the Coastal Plain and Piedmont regions *(16)*. It usually grows on dry ridgetops and upper slopes facing south and west, rather than on moist lower slopes and bottom lands, or north and east aspects *(16)*.

Associated Forest Cover

Southern red oak is found in nine forest cover types *(5)*. It is a major component of Virginia Pine-Oak (Society of American Foresters Type 78) and Shortleaf Pine-Oak (Type 76). It is a minor component of Virginia Pine (Type 79), Loblolly Pine-Shortleaf Pine (Type 80), Loblolly Pine (Type 81), and Loblolly Pine-Hardwood (Type 82). Occasionally it is

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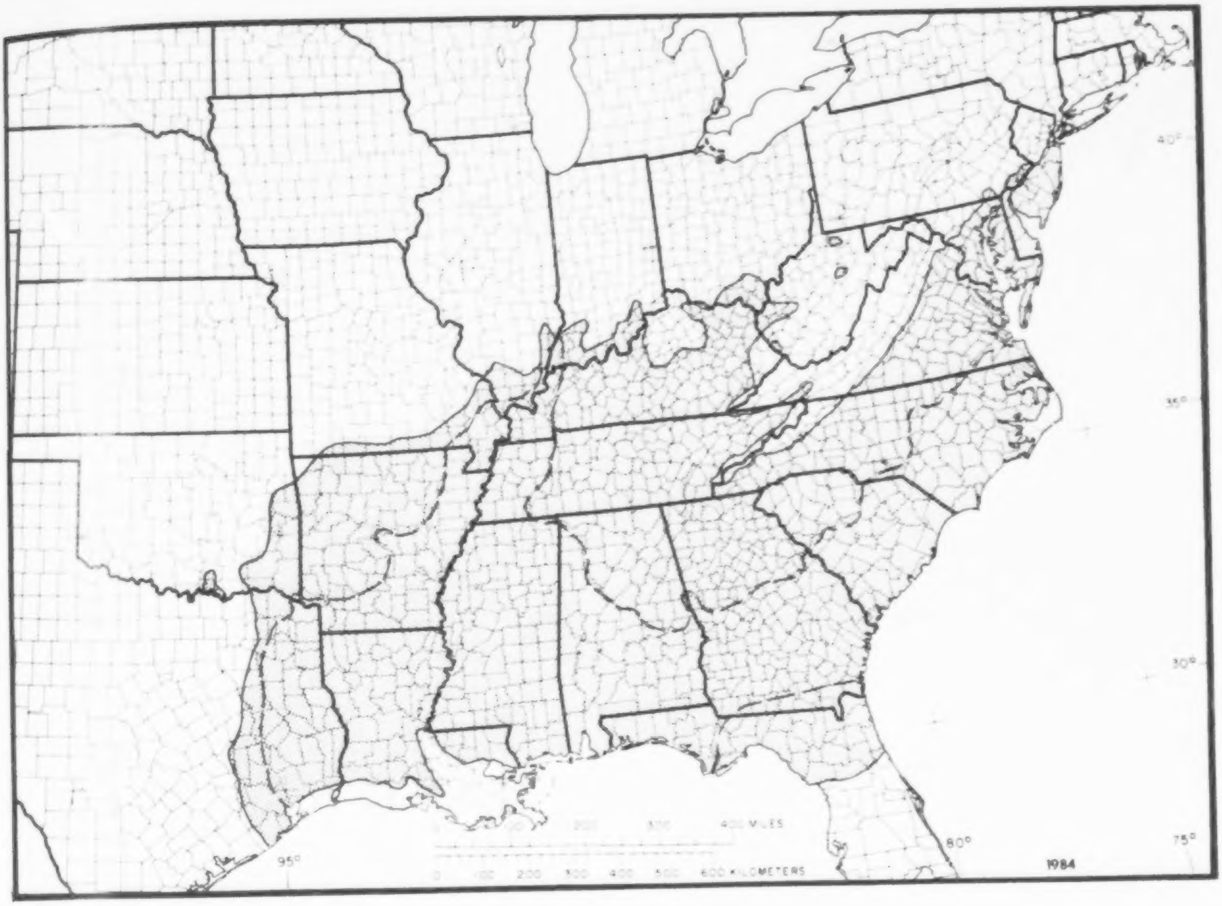

Figure 1—*The native range of southern red oak. Broken lines indicate the approximate northern and southern limits of cherrybark oak, which also grows in scattered localities northward.*

found with Longleaf Pine (Type 70), Swamp Chestnut Oak–Cherrybark Oak (Type 91), and Post Oak–Blackjack Oak (Type 40).

Throughout most of its range, southern red oak is usually found as individual trees in mixed stands. It is commonly associated with white oak (*Quercus alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), and hickory (*Carya* spp.). Along the foothills of the Appalachians, Virginia pine (*Pinus virginiana*), pitch pine (*P. rigida*), and chestnut oak (*Quercus prinus*) are common associates. Other associates are shortleaf pine (*Pinus echinata*) in the Piedmont, loblolly pine (*P. taeda*) in the Coastal Plain, and both shortleaf and loblolly pine in eastern Texas, southern Arkansas, and Louisiana.

Occasionally associated with southern red oak are swamp chestnut oak (*Quercus michauxii*), cherrybark oak (*Q. falcata* var. *pagodifolia*), white ash (*Fraxinus americana*), slash pine (*Pinus elliottii*), longleaf pine (*P. palustris*), yellow-poplar (*Liriodendron tulipifera*), southern magnolia (*Magnolia grandiflora*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), flowering dogwood (*Cornus florida*), and persimmon (*Diospyros virginiana*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Southern red oak is monoecious; unisexual flowers of both sexes are borne on the same tree. Flowering occurs during

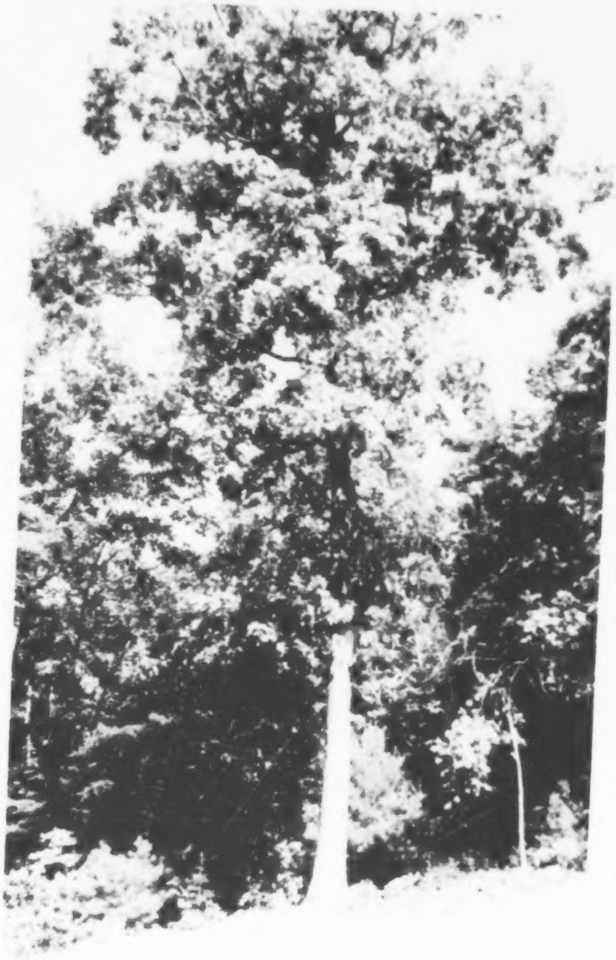

Figure 2—*Southern red oak.*

April and May throughout most of the range. The staminate flowers are borne in naked aments (catkins) and the pistillate flowers solitary, or in two- to many-flowered spikes.

The fruit is solitary or paired; the nut is enclosed one-third or less in a thin, shallow cup. The fruit ripens in September and October, the second season after flowering, and seedfall occurs during these months.

Seed Production and Dissemination—Seed production usually begins when a tree is about 25 years of age, but maximum production is usually between the ages of 50 and 75 years. Cleaned seeds average 1,190/kg (540/lb). Fall seeding of oaks is preferred to spring seeding in the nursery *(17)*. To obtain the highest first-year survival, it is recommended the acorns be planted not less than 1/2 inch deep and at seedbed densities of 12 to 15 evenly spaced sound seed per square foot *(13)*. Fall beds should be mulched with leaves or straw held in place by hardware cloth covers or other effective materials. The covering also serves as a protection against rodents. It is usually not necessary to produce seedlings older than 1-0 for field planting, but 2-0 seedlings are planted occasionally to obtain larger, vigorous stock with more extensive root systems.

In natural stands, dissemination of acorns by gravity is important on steep slopes. The hoarding habit of squirrels is also important in the dispersal of seed of oaks.

Seedling Development—The seed of southern red oak germinate under natural conditions in the spring following seedfall. Cool, moist stratification is required for best results. Germination is hypogeal *(17)*.

Vegetative Reproduction—Southern red oak sprouts vigorously from the stump when the top has been killed or cut back *(6,16)*. Sprouting is most prevalent on young stems 25.4 cm (10 in) or less in diameter. With well established root systems, growth of sprout-origin stands is rapid, regardless of site quality, for about 20 years *(18)*. Equations have been developed using sprout height at age 5 which predict the diameter growth and competition success of coppice-regeneration at ages 12 and 30 *(11)*. Clones of southern red oak can be propagated from cuttings of rooted stump sprouts and mature branches *(4)*. Cuttings from branches root better than cuttings from stump sprouts. Root initiation is increased when cuttings are treated with the growth hormone IBA and the fungicide folpet, and when cuttings 6.4 mm (0.25 in) or larger are taken from the first flush after it hardens off and just before second flush bud break. Survival after rooting is also increased when larger cuttings are used.

Sapling and Pole Stages to Maturity

Growth and Yield—At maturity, southern red oak is a medium-size tree, usually from 20 to 25 m (70 to 80 ft) in height and 60 to 90 cm (24 to 36 in) in d.b.h. In forest stands it develops a long, straight trunk and upward-reaching limbs that form a high, rounded crown *(16)*. Natural pruning is excellent in well-stocked stands *(19)*. Maximum age attained is about 150 years.

Equations are available for predicting green weights, dry weights, and green volume of sapling, pole-size and sawtimber southern red oak trees, using d.b.h. and total height classes *(3,12)*. Seventy percent of the average tree's green weight is in stem material to a 10-cm (4-in) top, and 30 percent is in crown material. Total-tree wood has an average specific gravity of 0.604, average moisture content of 74 percent, and average green weight of 1057 kg/cm^3 (66 lb/ft^3). The weight of wood and bark averages 1297 kg/m^3 (81 lb/ft^3) for the entire above-ground portion of the tree.

Growth and yield data are not available for stands of southern red oak.

Rooting Habit—No information available.

Reaction to Competition—Southern red oak is classed as intermediate in shade tolerance *(2)* or as intolerant *(16)*, when compared with its associates.

Epicormic branching is profuse on southern red oak, especially on recently released crop trees. This reduces the quality of the timber and suggests that good quality occurs only in dense stands.

The shelterwood method is recommended for regeneration *(7)*. Early removal of the overstory following stand establishment eliminates suppression from residual seed trees and prevents degrade from epicormic branching.

Damaging Agents—Southern red oak is susceptible to injury by fire because of its thin bark. As a result of fire scars and other injuries, this species often is subject to heart rots *(16)*. Cankers and rot caused by *Polyporus hispidus* are common. Other common rot fungi affecting this species include *Hydnum erinaceus*, *Polyporus sulphureus*, *P. obtusus*, and *Fomes everhartii*.

While southern red oak is highly susceptible to oak wilt caused by *Ceratocystis fagacearum*, this disease is virtually unknown south of the 35th parallel *(9)*. Several species of *Hypoxylon* have been found to colonize the trunk sapwood of wilting trees, producing a yellow decay *(14)*. Apparently *Ceratocystis fagacearum* is unable to compete with the *Hypoxylon* spp.

Drought has been identified as a cause of southern red oak decline and death along the South Carolina coast *(15)*. *Hypoxylon atropunctatum* was also partially responsible for these losses.

Leaf blister caused by *Taphrina caerulescens* and leaf spots caused by *Actinopelte dryina* or *Elsinoe quercus-falcatae* can severely mar the foliage of southern red oak *(9)*.

The seedlings are damaged and often killed by the hickory spiral borer, *Agrilus arcuatus torquatus*, and the oak stem borer, *Aneflormorpha subpubescens (16)*.

As in many of the oaks, the acorn is subject to damage by acorn weevils, such as *Curculio longidens*, *C. pardalis*, and *Conotrachelus posticatus*, and the filbertworm, *Melissopus latiferreanus*.

Southern red oak is readily susceptible to borers and bark scarrers when trees are wounded or growing on poor sites. Wood-boring insects attacking this tree are *Agrilus bilineatus*, *Corthylus columbianus*, and *Cossula magnifica*. The defoliators *Anisota senatoria* and *A. stigma* also do considerable damage.

Special Uses

The uses of oak include almost everything that mankind has ever derived from trees—timber, food for man and animals, fuel, watershed protection, shade and beauty, tannin, and extractives *(17)*.

Genetics

Nine hybrids of southern red oak have been recognized *(10)*. They are crosses with *Q. ilicifolia* (*Q.* × *caesariensis* Moldenke); *Q. imbricaria* (*Q.* × *anceps* Palmer); *Q. incana* (*Q.* × *subintegra* Trel.); *Q. laevis* (*Q.* × *blufftonensis* Trel.); *Q. laurifolia* (*Q.* × *beaumontiana* Sarg.); *Q. marilandica*; *Q. nigra* (*Q.* × *garlandensis* Palmer); *Q. phellos* (*Q.* × *ludoviciana* Sarg.); *Q. velutina* (*Q.* × *wildenowiana* (Dippel) Zabel, *Q.* × *pinetorum* Moldenke).

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CHERRYBARK OAK

Cherrybark oak *(Quercus falcata* var. *pagodifolia)*, also called bottomland red oak, red oak, swamp red oak, swamp Spanish oak, and Elliott oak, is the high-value red oak in the South. It is larger and better formed than southern red oak and commonly grows on more moist sites. The heavier stronger wood makes it an excellent timber tree; it is used for furniture and interior finish. Many wild animals and birds use the acorns as food. This tree is also a pleasant shade tree.

Habitat

Native Range

Cherrybark oak (fig. 1) is found in the Atlantic and Gulf Coastal Plain, from southeastern Virginia to northwestern Florida; west to eastern Texas; and north in the Mississippi Valley to extreme southeastern Oklahoma, southeastern Missouri, southern Illinois and southwestern Indiana *(26)*.

Climate

Cherrybark oak grows in a humid, temperate climate characterized by hot summers and mild winters. Through most of the tree's range, the growing season varies from 210 to 280 days, with average annual temperatures of 16° to 21° C (60° to 70° F). Average annual precipitation ranges from 1140 to 1520 mm (45 to 60 in) *(38)*. The lower Mississippi Valley tends to have less growing season rainfall and therefore more frequent droughts during the summer than the Atlantic Coastal Plain *(25)*.

Soils and Topography

Cherrybark oak is widely distributed on the best loamy sites on first bottom ridges and on well-drained terraces and colluvial sites *(27)*. These sites occur along both large and small streams of the Southeastern Coastal Plain and the Mississippi Valley north into Missouri and Illinois, although the tree is rare in the lower Mississippi Delta.

Cherrybark oak develops best on a loamy well-drained soil. Although uncommon on clay soils, it is generally of good form and quality on such soils if the drainage is good but very inferior where drainage is poor. Cherrybark oak is found mostly where surface soil pH is acid to medium acid *(10)*. It is a lowland tree but is seldom numerous on wet or swampy soils.

Cherrybark oak also grows in Coastal Plain hummocks. These localized areas, which may be raised above surrounding terrain, are not necessarily associated with any stream but are usually well drained and have a deep soil of good texture. The species is also found on certain upland sites. Included are areas of loessial soil such as the Brown Loam Bluffs bordering the eastern edge of the Mississippi River alluvial plain from Louisiana north. Other favorable sites are found in the rolling hills of the lower Piedmont and certain uplands of the upper Coastal Plain. Here the species grows well in branch heads, coves, and slopes with deep surface soils *(27)*.

Overall, cherrybark oak grows most commonly on soils of the order Alfisols and Inceptisols.

A site index predictive model for cherrybark oak based on measurable soil variables accounted for less than half the variation in site index. Most significant soil variables were depth to mottling, depth of topsoil, and presence or absence of fragipan *(9)*.

A combined objective and subjective approach to site evaluation for cherrybark oak plantations has been developed that is based on soil physical conditions, nutrient availability, moisture availability during the growing season, and aeration. Site index values obtained should be within 1.5 m (5 ft) of measured values 95 percent of the time *(2)*.

Associated Forest Cover

The main forest cover type that includes cherrybark oak is Swamp Chestnut Oak–Cherrybark Oak (Society of American Foresters Type 91) *(14)*. Typically the composition varies widely, and cherrybark oak and swamp chestnut oak *(Q. michauxii)* are often only indicator trees, although they may be the most abundant of the oaks present. Other prominent tree species are white ash *(Fraxinus americana)*, shagbark hickory *(Carya ovata)*, shellbark hickory *(C. laciniosa)*, mockernut hickory *(C. tomentosa)*, and bitternut hickory *(C. cordiformis)*. Less numerous are blackgum *(Nyssa sylvatica)*, white oak *(Q. alba)*, Delta post oak *(Q. stellata* var. *paludosa)*, and Shumard oak *(Q. shumardii)*. On first bottom ridges sweetgum *(Liquidambar styraciflua)* may be important. Minor associates include southern red oak *(Q. falcata* var. *falcata)*, southern magnolia *(Magnolia grandiflora)*, yellow-poplar *(Liriodendron tulipifera)*, American beech *(Fagus grandifolia)*, willow oak *(Q. phellos)*, water oak *(Q. nigra)*, post oak *(Q. stellata)*, American elm *(Ulmus americana)*, winged elm *(U. alata)*, water hickory *(C. aquatica)*, nutmeg hickory *(C. myristiciformis)*, and occasionally loblolly pine *(Pinus taeda)* and spruce pine *(P. glabra)*.

This cover type is widely distributed over the alluvial flood plains of the major rivers, occurring on all ridges in the terraces and on the best, most mature, fine sandy loam soils on the highest first bottom ridges. It extends on first bottom ridges to a few well-drained soils other than sandy loam. These sites are seldom covered with standing water, although, if there are hummocks, the sites between them may be wet.

White oak is the predominant tree in Swamp Chestnut Oak–Cherrybark Oak on the most mature terrace soils. In very limited situations cherrybark oak is found with loblolly pine on terraces, and with spruce pine on terraces and stream fronts and ridges in the first bottoms of small streams of the Coastal Plain east of the Mississippi River. It is found with yellow-poplar and beech only in the second bottoms of small secondary streams and in the Brown Loam Bluffs.

Cherrybark oak may be an associated tree on better drained areas in the cover type Willow Oak–Water Oak–Diamondleaf Oak (Type 88) and on moist sites in Loblolly Pine (Type 81) and Loblolly Pine–Hardwood (Type 82).

Other trees associated with cherrybark oak are red buckeye *(Aesculus pavia)*, devils-walkingstick *(Aralia spinosa)*, American hornbeam *(Carpinus caroliniana)*, red mulberry *(Morus rubra)*, southern bayberry *(Myrica cerifera)*, Carolina basswood *(Tilia caroliniana)*, eastern hophornbeam *(Ostrya virginiana)*, pawpaw *(Asimina triloba)*, eastern redbud *(Cercis canadensis)*, flowering dogwood *(Cornus florida)*, witch-hazel *(Hamamelis virginiana)*, American holly *(Ilex opaca)*, hawthorns *(Crataegus* spp.), Hercules-club *(Zanthoxylum clava-herculis)*, roughleaf dogwood *(Cornus drummondii)*, and snowbell *(Styrax* spp.) *(27,30)*.

Common understory plants include giant cane *(Arundinaria gigantea)*, blackberry *(Rubus* spp.), and hydrangeas *(Hydrangea* spp.), along with vines such as redberry moonseed *(Cocculus carolinus)*, southeast decumaria *(Decumaria barbara)*, peppervine *(Ampelopsis arborea)*, Virginia creeper *(Parthenocissus quinquefolia)*, and grape *(Vitis* spp.) *(30)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Cherrybark oak is monoecious; staminate and pistillate catkins are borne separately on the same tree, with the staminate catkins clustered and the pistillate flowers in a solitary position or several together. They are borne on stalks from leaf axils of the current growth. The flowers appear from February to May, depending on latitude. The acorn is about 13 mm (0.5 in) long, globular or hemispheric, with up to one-third of its length enclosed in a shallow thin cap. Seeds per kilogram range from 440 to 1,650 (200 to 750/lb). Acorns mature from August to November of the second year. In central Mississippi, acorns in their second year grew at a steady rate from June through August. Maximum acorn size was reached in September as storage food content increased rapidly and moisture content dropped from 60 to 40 percent. At full physiological maturity, in late October or early November, acorns had attained maximum dry weight and were dark brown, easily separated from their cups, 15 to 20 percent crude fat, 25 percent carbohydrate, and 35 to 40 percent moisture *(7)*.

The best method of determining germinability of cherrybark oak acorns is by flotation combined with visual inspection. Both floaters and those with weevil blemishes on the shell or dark, dull cup scars are considered nonviable *(8)*.

Moisture content of cherrybark oak acorns is a critical factor. Acorns stratified over winter and then air-dried for more than 4 days did not germinate. Therefore, fall-collected acorns should either be sowed immediately or promptly placed in moist cold storage *(23)*.

Cherrybark oak acorns may be stored for up to 18 months at temperatures slightly above freezing if the seeds, at 45 to 50 percent moisture content, are kept in polyethylene bags of at least 0.01 cm (4 mils) thickness, although some will sprout during storage *(6)*.

One study showed that the germination percentage of cherrybark oak acorns is significantly reduced by submersion in water for 34 days *(27)*.

Seed Production and Dissemination—Seedbearing begins when the trees are about 25 years old, and optimum production is reached when they are between 50 and 75 years of age. Good crops are frequent, occurring at 1- or 2-year intervals, with light crops in intervening years. A freeze in April 1955, after the flower buds opened, resulted in a complete crop failure over much of the tree's range in 1956. Dissemination largely depends on hoarding activity of animals, especially squirrels. In certain situations (first bottoms) dissemination by flooding is possible. Gravity is a minor means of dissemination on the steeper terrace margins *(27)*.

Seedling Development—Cherrybark oak regenerates naturally on areas protected from fire and grazing. Being intolerant of shade, it requires full light for development, which in turn induces heavy competition from annual weeds, vines, briars, and brush. It often makes its best development in old fields on well-drained loamy soils *(27)*. Typically, seeds remain dormant after falling and do not germinate until the following spring. Germination is hypogeal.

Several studies have involved direct seeding of cherrybark oak acorns. Repellents (arasan, endrin, and anthraquinone) were found to reduce germination *(4)*. One recommendation was to sow 4,940 acorns per hectare (2,000/acre) to obtain 1,230 established seedlings per hectare (500/acre), although elimination of weeviled acorns would reduce seed requirements *(21)*. In South Carolina, direct seeded acorns averaged 30 percent survival, with seedlings 51 cm (20 in) tall after 3 years on sandy loam soils associated with first and second bottoms of small coastal streams. Height growth, which was greater in the open than in the shade, was indicative of natural regeneration development *(27)*. In an Arkansas trial, only 2 percent of cherrybark oak acorns seeded under a deadened low-quality gum and oak stand resulted in established seedlings. High germination over a 3-month period was negated by grass competition, heavy grazing, and severe drought *(11)*. Success of direct seeding in starting stands, therefore, is dependent on favorable climatic and soil conditions together with limited plant and animal competition.

Cherrybark oak seedling development has been studied in nurseries and outplantings. The highest percentage of plantable seedlings per unit weight of seeds came from the lowest seedbed density, where densities varied from 43 to 108 seedlings per square meter (4 to 10/ft²) *(3)*. Survival of cherrybark oak seedlings decreased as severity of root and top pruning increased *(40)*. Seedlings started in kraft paper tubes had less growth and survival than bare rooted seedlings when outplanted. The container seedlings were smaller and the tubes restricted root growth *(22)*. In another test of seedlings planted in containers, it was found that after 3 years, those seedlings planted with bare roots or in milk cartons had a better survival rate than those that had been planted in cardboard tubes *(33)*.

Pot planting studies of first-year seedlings rated cherrybark oak intolerant of flooding and saturated soils. Seedlings did not develop adventitious roots, as did tolerant species, and leaf mortality was related to moisture deficits *(18,19,20)*.

A 1-percent solution of gibberellic acid in lanolin applied to new shoot growth of 1-year-old seedlings significantly increased height growth over a 41-day observation period *(31)*.

Growth of planted cherrybark oak seedlings in minor bottoms has been variable, but best growth is usually obtained where vegetative competition is controlled by cultivation. In an Arkansas planting, trees disked annually averaged 4.3 m (14 ft) in 5 years, with 75 percent survival *(24)*. Trees planted in Louisiana were 2.4 m (8 ft) tall after 6 years, and 4.9 m (16 ft) tall after 9 years, with 93 percent survival *(1)*. A Carolina coastal plain planting of cherrybark oak averaged 1.4 m (4.6 ft) and 46 percent survival after 5 years *(36)*.

In a test where site preparation consisted of deadening residuals, planted cherrybark oaks were smaller and fewer in number than the natural regeneration after 11 years *(13)*.

Amount of cherrybark oak reproduction is mainly determined by seed supply but is also influenced by microclimate, soil factors, and stand variables. Seedling development is related to overhead release, with large openings needed *(17)*.

Restricted understory development beneath cherrybark oak trees is apparently caused by leaching of salicylic acid, an inhibitor, from the oak crowns by rain. Reduced germination and growth of seedlings was also shown in greenhouse studies using soil obtained from under cherrybark oak trees *(12)*.

Vegetative Reproduction—The tree is reported to sprout from the stump when the shoot has been killed or cut back *(27)*. However, sprouting is not considered a dependable means for obtaining desirable natural regeneration. Seedlings and smaller trees (advance reproduction) sprout more than larger trees, and more sprouting occurs on lower quality sites. Like most oaks, this species is difficult to propagate by cuttings, although in Mississippi air layering has succeeded in April and June *(5)*. Greenwood apical cuttings from 1- to 4-month-old cherrybark oak seedlings have been rooted in 4 weeks under mist after treatment with indolebutyric acid *(15)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Cherrybark oaks (fig. 3) often attain heights and diameters of 30.5 to 39.6 m and 91 to 152 cm (100 to 130 ft and 36 to 60 in), respectively, which classes them with the largest of the southern red oaks. It is one of the hardiest and fastest growing oaks and grows well on more sites than any other bottom-land oak except the willow and water oaks. Diameter growth rates range from 7 to 15 cm (3 to 6 in) in 10 years *(27)*. As a guide, the maximum gross cubic volume growth per year has been estimated to range from 13 to 19 m^3/ha (188 to 275 ft^3/acre) on good sites (site indexes from 32 to 40 m (105 to 130 ft) at base age 50). Only one-half to two-thirds of these yields could be expected from good extensive management practices *(32)*.

Rooting Habit—Cherrybark oak is classified as having poor windfirmness *(30)*. In the root system of most oaks, the taproot dies back and sinker roots arising from the laterals take over the vertical root function.

Reaction to Competition—Cherrybark oak is often found as individual trees in mixed stands but is sometimes found in groups, and occasionally, with Shumard oak, it dominates a stand. It cannot live under complete shade, however, and is usually found in a dominant or codominant position. It is classed as intolerant of shade and probably becomes established only in openings *(27)*.

This oak usually has a relatively branch-free merchantable bole in contrast with other bottom-land red oaks such as pin and willow oak. Often it is conspicuous for this reason, and because of its good form and quality it is regarded as one of the best red oaks *(27)*.

Following release or injury this oak produces epicormic sprouts but to no greater degree than many other oaks.

Damaging Agents—Wood-boring insects often cause much damage in fire-scarred cherrybark oaks and in overmature trees. Moreover, on poorly drained clay flats or other poor sites, the mature trees are often infested with borers or the wood is mineral streaked. Fires and hurricane winds seem to be instrumental in introducing the borers and mineral streaks *(27)*.

Trunk boring insects found in cherrybark oak are the carpenterworm *(Prionoxystus robiniae)*, red oak borer *(Enaphalodes rufulus)*, oak clearwing borer *(Paranthrene simulans)*, and the living-beech borer *(Goes pulverulentus) (34,35)*. Oak twig galls (multiple species) are a common occurrence in the loessial hills and coastal plain sites. Insects identified as attacking southern red oak probably also attack cherrybark oak; these are the defoliating Anisota oakworms *(Anisota* spp.), the twolined chestnut borer *(Agrilus bilineatus)*, Columbian timber beetle *(Corthylus columbianus)*, and pecan carpenterworm *(Cossula magnifica)*. Other probable cherrybark oak insects are the hickory spiral borer *(Agrilus arcuatus* var.

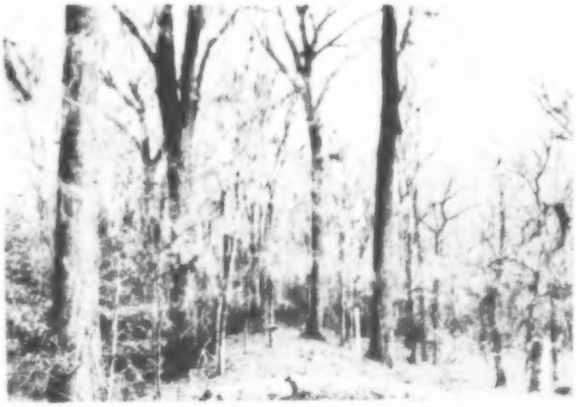

Figure 3—*Large cherrybark oak trees in South Carolina.*

torquatus) and the oak-stem borer *(Aneflormorpha subpubescens) (27).*

Hispidus canker *(Polyporus hispidus)* is common on cherrybark oak. Rot fungi attacking southern red oak and possibly cherrybark oak are *Hericium erinaceus, Laetiporus sulphureus,* and *Daedalea quercina.* Leaf blister caused by *Taphrina caerulescens* occurs frequently. Cherrybark oak is susceptible to oak wilt *(Ceratocystis fagacearum) (27,28,29,39).* Heart rot in standing cherrybark oak trees generally is greater on poor sites than on good sites *(37).*

As in most of the oaks, the acorn is subject to damage by nut or acorn weevils, such as *Curculio baculi, C. longidens, C. pardalis,* and *Conotrachelus posticatus,* and the filbertworm *(Melissopus latiferreanus) (27).*

Pine voles have destroyed cherrybark oak seedlings in outplantings in the loess hills.

Special Uses

Within the range of this oak, animals and birds include acorns as a substantial part (10 percent or more) of their diets. Among these the heaviest eaters are the gray squirrel, wild turkey, and blue jay, followed by the wood duck, red-bellied woodpecker, red-headed woodpecker, white-breasted nuthatch, common grackle, raccoon, white-tailed deer, and eastern fox squirrel *(27).*

Genetics

Stands of cherrybark oak in west Tennessee and central Mississippi averaged 0.601 specific gravity and 1.49 mm (0.06 in) fiber length. Most variation was from tree-to-tree differences within stands, indicating that field selection of breeding material should be on an individual tree basis *(16).*

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Quercus garryana Dougl. ex Hook. Oregon White Oak

Fagaceae Beech family

William I. Stein

Oregon white oak (*Quercus garryana*), a broad-leaved deciduous hardwood common inland along the Pacific Coast, has the longest north–south distribution among western oaks—from Vancouver Island, British Columbia, to southern California. It is the only native oak in British Columbia and Washington and the principal one in Oregon. Though commonly known as Garry oak in British Columbia, elsewhere it is usually called white oak, post oak, Oregon oak, Brewer oak, or shin oak. Its scientific name was chosen by David Douglas to honor Nicholas Garry, secretary and later deputy governor of the Hudson Bay Company.

Habitat

Native Range

The range of Oregon white oak (fig. 1) spans more than 15° of latitude from just below the 50th parallel on Vancouver Island in Canada south nearly to latitude 34° N. in Los Angeles County, CA. South of Courtenay, BC. Oregon white oak is common in the eastern and southernmost parts of Vancouver Island and on adjacent smaller islands from near sea level up to 200 m (660 ft) or more *(47)*. It is not found on the British Columbia mainland except for two disjunct stands in the Fraser River Valley *(28)*. In Washington, it is abundant on islands in Puget Sound and distributed east and west of the Sound and then south and east to the Columbia River at elevations up to 1160 m (3,800 ft) *(68)*. Oregon white oak is widespread at lower elevations in most of the Willamette, Umpqua, and Rogue River Valleys of western Oregon *(67,68)*. It is also common in the Klamath Mountains and on inland slopes of the northern Coast Ranges in California to San Francisco Bay but infrequent from there southward to Santa Clara County *(29)*.

In small tree and shrub sizes, Oregon white oak extends inland to just east of the Cascade Range, mainly in the Columbia River and Pit River drainages *(29,50,67,68,71)*. It has a scattered distribution the entire length of the western Sierra Nevada south to the Tehachapi Mountains in Kern and northern Los Angeles Counties where it forms extensive brush fields at elevations up to 2290 m (7,500 ft) *(29,76)*.

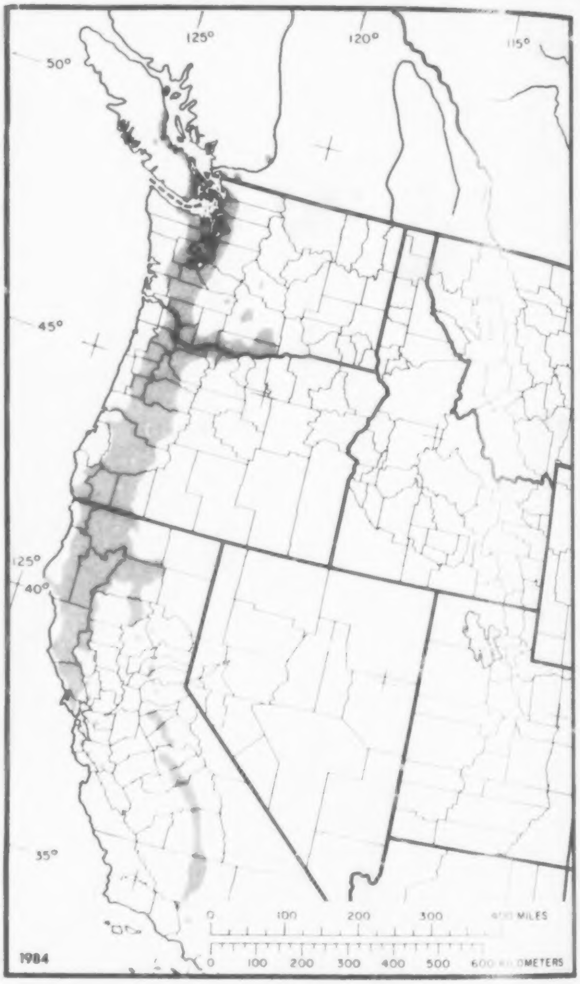

Figure 1—*The native range of Oregon white oak.*

Climate

Oregon white oak grows in diverse climates, ranging from the cool, humid conditions near the coast to the hot, dry environments in inland valleys and foothill woodlands. Records from 48 climatic observation stations within or bordering its range indicate that Oregon white oak has endured temperature ex-

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tremes of −34° to 47° C (−30° to 116° F) *(45,47,53,77)*. Average annual temperatures range from 8° to 18° C (46° to 64° F); average temperatures in January, from −11° to 10° C (13° to 50° F); and in July, from 16° to 29° C (60° to 84° F).

Average annual precipitation ranges from 170 mm (6.7 in) at Ellensburg, WA, east of the Cascades to 2630 mm (103.5 in) at Cougar, WA, west of the Cascades. Precipitation at the southern end of the range of Oregon white oak (Tehachapi) averages 270 mm (10.6 in), similar to that at northerly locations east of the Cascades—Ellensburg, Yakima, and Goldendale in Washington and The Dalles and Dufur in Oregon. Average annual snowfall ranges from little, if any, at several locations to 417 cm (164 in) at Mineral in Tehama County, CA. Average precipitation in the growing season (April through September) ranges from 30 mm (1.2 in) at Tehachapi, CA, and Ellensburg, WA, to 630 mm (24.8 in) at Cougar, WA. Length of average frost-free season (above 0° C; 32° F) ranges from 63 days at Burney in Shasta County, CA, to 282 days at Victoria, BC.

Soils and Topography

Oregon white oak can grow on a wide variety of sites, but on good sites it is often crowded out by species that grow faster and taller. Hence, Oregon white oak is most common on sites that are too exposed or droughty for other tree species during at least part of the year, including inland valleys and foothills, south slopes, unglaciated and glaciated rocky ridges, and a narrow transition zone east of the Cascades between conifer forest and treeless, dissected plateau. Although usually considered a xeric species, Oregon white oak also commonly occurs in very moist locations—on flood plains, on heavy clay soils, and on river terraces. These locations appear to have two common characteristics—standing water or a shallow water table during a lengthy wet season and gravelly or heavy clay surface soils that probably are droughty during the extended dry season. The distribution of Oregon white oak gives evidence that it can withstand both lengthy flooding and drought.

Oregon white oak grows on soils of at least four orders: Alfisols, Inceptisols, Mollisols, and Ultisols. Specific soil series include Hugo and McMahon in coastal northern California and Goulding near Santa Rosa *(75,78)*. In Oregon's Willamette Valley, Oregon white oak is found on soils derived from alluvial deposits (poorly drained gray brown Amity and Dayton series), sedimentary rocks (deep, well-drained brown Steiwer, Carlton, Peavine, Bellpine, Melbourne, and Willakenzie series), and basic igneous rocks (brown or reddish, moderately deep, well-drained Nekia, Dixonville, and Olympic series) *(22,38,67,73)*. A subsurface clay layer that restricts water penetration is characteristic of soils in most of these series. White oak stands near Dufur in eastern Oregon grow in soils derived from basalt and andesite *(32)*; in southern Oregon, they grow in soils derived from andesite, granite, and serpentine *(79)*. On the southeastern tip of Vancouver Island, BC, seven soils supporting a vegetational sequence of grass, Oregon white oak, and Douglas-fir were gravelly loams or gravelly sandy loams that developed on young, nonhomogeneous parent materials *(11)*.

Soils under Oregon white oak stands are generally acidic, ranging in pH from 4.8 to 5.9 *(11,75,78)*. Bulk densities ranging from 0.61 to 1.45 have been measured *(73,78)*. Many white oak stands grow on gentle topography; only one-fourth of those examined in the Willamette Valley were on slopes greater than 30 percent *(73)*.

Associated Forest Cover

Oregon white oak is found in pure, closed-canopy stands; in mixture with conifers or broad-leaved trees; and as scattered single trees or groves on farmlands, woodlands, and prairies (fig. 2). It grows to large sizes but is also found extensively as scrub forest. The best stands are in western Oregon and Washington—in the Cowlitz, Lewis, and Willamette River drainages—but stands or trees with substantial volume are found from British Columbia to central California. Dense dwarf or shrub stands of

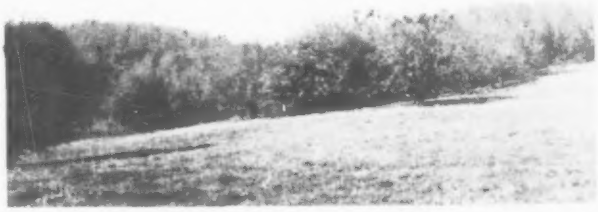

Figure 2—*Pure oak woodland on a ranch in the Willamette Valley, OR. Hairy mistletoe plants* (Phoradendron villosum) *are prominent in the leafless treetops.*

Oregon white oak, earlier identified as *Quercus garryana* var. *breweri*, and other stands previously identified as *Q. garryana* var. *semota*, form dense thickets over large areas in California *(29,35,57,76,81)*. Similar dwarf or shrub forms grow to a more limited extent on severe sites in the rest of its range *(57,79)*.

Oregon white oak is recognized as a distinct forest cover type (Society of American Foresters Type 233) and is listed as an associated species in at least eight other forest cover types *(20)*: Pacific Douglas-Fir (Type 229), Port Orford-Cedar (Type 231), Redwood (Type 232), Douglas-Fir–Tanoak–Pacific Madrone (Type 234), Pacific Ponderosa Pine (Type 245), California Black Oak (Type 246), Knobcone Pine (Type 248), and Blue Oak–Digger Pine (Type 250). Its prominence and occurrence in these types, as well as in several others for which it is not specifically listed, vary widely.

Plant communities have been identified in parts of the Oregon white oak type. A Garry oak community of two types (oak parkland and scrub oak-rock outcrop), a Garry oak-arbutus, and an arbutus-Garry oak community have been defined in the Victoria, BC, metropolitan area *(42)*. Four communities, ranked in order from wettest to driest, have been identified in white oak forests of the Willamette Valley: Oregon white oak/California hazel/western swordfern, Oregon white oak/sweet cherry/common snowberry, Oregon white oak/Saskatoon serviceberry/common snowberry, and Oregon white oak/Pacific poison-oak *(73)*. These communities are floristically similar, being differentiated primarily by the relative coverage and frequency of a few shrub species. Five Oregon white oak communities identified in the North Umpqua Valley of Oregon were similar to the xeric Oregon white oak/Pacific poison-oak association of the Willamette Valley; a sixth was a riparian association dominated by Oregon white oak and Oregon ash (*Fraxinus latifolia*) *(62)*. In California, four communities dominated by Oregon white oak were found in the Bald Hills woodlands of Redwood National Park *(70)* and three communities dominated by Oregon white oak or related hybrids were identified in a limited area on Bennett Mountain *(75)*. The shin oak brush association, largely composed of Oregon white oak, is a distinctive plant community in Kern and Los Angeles Counties *(76)*.

The composition of Oregon white oak communities varies greatly because of differences in soil, topography, and climate, and in fire and grazing histories. Because of proximity to farmlands, many communities include introduced forbs and grasses. Pacific poison-oak (*Rhus diversiloba*) and common snowberry (*Symphoricarpos albus*) are probably the most widespread and characteristic shrub associates. Species often found with Oregon white oak are listed in table 1. The listing is not exhaustive; it just indicates the great variety of common associates. Species associated with Oregon white oak in chaparral communities and on serpentine soils are listed in other sources *(15,16,79)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Oregon white oak flowers somewhat later in the spring than many of its associates. Flowering has been noted in March, April, May, and June *(72,74)*, but the seasonal span is probably greater over the wide range of latitudes and elevations where this species occurs. Flowers appear concurrently with new leaves and extension of twig growth.

The species is monoecious, bearing slim, staminate flowers (catkins) that emerge from buds on existing twigs and also appear on the basal end of developing twigs *(64)*. Some catkins associated with new twig growth just originate from the same bud; others are located as much as 5 mm (0.2 in) from the base on new growth. Catkins are pale yellow tinged with green. Fully extended catkins vary greatly in length—in one collection, from 3 to 10 cm (1.2 to 3.9 in). Catkins of the same twig and cluster are in various stages of development—some are fading before others reach full size. The faded dry catkin is light brown and fragile.

The closed pistillate flowers are small, deep red, and covered with whitish hairs *(64)*. They appear in axils of developing leaves, either single and sessile or as many as five or six on a short stalk up to 2 cm (0.8 in) long. Two flowers are often located at the base of the stalk and several along and at its tip. Basal flowers may be open while others on the stalk are still tiny and tightly closed. Flower openings are narrow; the interior elements are greenish to yellowish. Flowers were found on new growth that had extended only 1 cm (0.4 in) or up to 12 cm (4.7 in); most flowers were on new growth 4 to 7 cm (1.6 to 2.8 in) long. Flowering appears at its fullest when the first leaves are about half size; when leaves approach full size, catkins are withered. On a single tree, flowering seems to be a short event, perhaps a week long, as leaves develop quickly once growth starts.

Individual trees are known to flower abundantly, but observations are needed on the regularity of flowering and on the variability within and between stands and locations.

Table 1—Trees, shrubs, and herbs associated with Oregon white oak in different parts of its range[1]

Trees	Shrubs	Herbs
Abies grandis	*Amorpha californica*	*Agropyron spicatum*
Acer circinatum	*Arctostaphylos columbiana*	*Agrostis* spp.
Acer glabrum	*Arctostaphylos manzanita*	*Allium* spp.
Acer macrophyllum	*Arctostaphylos media*	*Athysanus pusillus*
Aesculus californica	*Arctostaphylos uva-ursi*	*Avena barbata*
Alnus rubra	*Berberis aquifolium*	*Balsamorhiza deltoides*
Amelanchier alnifolia	*Berberis nervosa*	*Brodiaea* spp.
Arbutus menziesii	*Ceanothus cuneatus*	*Bromus* spp.
Betula occidentalis	*Ceanothus integerrimus*	*Camassia* spp.
Castanopsis chrysophylla	*Ceanothus velutinus*	*Carduus pycnocephalus*
Cercocarpus betuloides	*Cornus stolonifera*	*Carex* spp.
Cornus nuttallii	*Crataegus oxyacantha*	*Chlorogalum pomeridianum*
Corylus cornuta	*Cytisus scoparius*	*Collinsia* spp.
Crataegus douglasii	*Gaultheria shallon*	*Crocidium multicaule*
Fraxinus latifolia	*Hedera helix*	*Cynosurus echinatus*
Heteromeles arbutifolia	*Holodiscus discolor*	*Dactylis glomerata*
Juniperus scopulorum	*Osmaronia cerasiformis*	*Danthonia californica*
Libocedrus decurrens	*Philadelphus lewisii*	*Delphinium menziesii*
Lithocarpus densiflorus	*Physocarpus capitatus*	*Dentaria californica*
Pinus contorta	*Purshia tridentata*	*Dodecatheon hendersonii*
Pinus monticola	*Rhus diversiloba*	*Dryopteris arguta*
Pinus ponderosa	*Ribes sanguineum*	*Elymus glaucus*
Pinus sabiniana	*Rosa eglanteria*	*Eriogonum nudum*
Populus tremuloides	*Rosa gymnocarpa*	*Eriophyllum lanatum*
Populus trichocarpa	*Rosa nutkana*	*Erythronium oregonum*
Prunus avium	*Rubus laciniatus*	*Festuca* spp.
Prunus emarginata	*Rubus parviflorus*	*Fritillaria lanceolata*
Prunus virginiana	*Rubus procerus*	*Galium* spp.
Pseudotsuga menziesii	*Rubus ursinus*	*Holcus lanatus*
Pyrus communis	*Spiraea betulifolia*	*Hypericum perforatum*
Pyrus fusca	*Spiraea douglasii*	*Lathyrus* spp.
Pyrus malus	*Symphoricarpos albus*	*Lomatium utriculatum*
Quercus agrifolia	*Symphoricarpos mollis*	*Lonicera ciliosa*
Quercus chrysolepis	*Symphoricarpos rivularis*	*Lotus micranthus*
Quercus douglasii	*Vaccinium ovatum*	*Lupinus* spp.
Quercus kelloggii	*Vaccinium parvifolium*	*Melica geyeri*
Rhamnus purshiana	*Viburnum ellipticum*	*Mimulus* spp.
Salix spp.		*Montia* spp.
Sambucus cerulea		*Nemophila heterophylla*
Taxus brevifolia		*Osmorhiza* spp.
Thuja plicata		*Phacelia linearis*
Tsuga heterophylla		*Platyspermum scapigera*
Umbellularia californica		*Plectritis* spp.
		Poa pratensis
		Polystichum munitum
		Pteridium aquilinum
		Ranunculus spp.
		Sanicula crassicaulis
		Sedum spathulifolium
		Sherardia arvensis
		Silene californica
		Sisyrinchium douglasii
		Stipa spp.
		Thysanocarpus curvipes
		Trifolium tridentatum
		Vicia americana
		Viola ocellata
		Zigadenus venenosus

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[1] Sources: 2,10,11,13,20,22,24,28,31,32,35,42,47,54,62,63,67,69,70,71,72,73,75,78

Seed Production and Dissemination—Seed crops may be heavy but are considered irregular. The large acorns, typically about 3 cm (1.2 in) long and half as wide, mature in one season and ripen from late August to November. The age when a tree first bears fruit, the age of maximum production, and the average quantity produced have not been determined. In one collecting effort, about 18 kg (40 lb) of acorns per hour could be hand-picked from the ground under woodland trees between Redding and Weaverville, CA. The yield was estimated to be 5 to 9 kg (10 to 20 lb) each for trees 3 to 9 m (10 to 30 ft) tall and 15 to 30 cm (6 to 12 in) in diameter; production for this fair crop was about 560 kg/ha (500 lb/acre) *(81)*. Northeast of Mount Shasta, a fair crop the same year yielded about 23 kg (50 lb) of acorns from a single tree 8 m (25 ft) in height and crown spread. In the Willamette Valley, acorns were dispersed from September to November, and three crops ranged from failure to 1737 kg/ha (1,550 lb/acre) ovendry-weight basis *(12)*. Large crops of acorns are also produced by shrubby forms of Oregon white oak, but density of the stands can make collection difficult.

The heavy seeds disseminate by gravity only short distances from the tree crowns, except on steep slopes. Local transport is attributed primarily to the food-gathering activities of animals. In the past, Indians—and also pigeons—may have been responsible for long-distance colonization of Oregon white oak *(28,71)*.

Seedling Development—Acorns of Oregon white oak must be kept moist until they germinate. In nature, moisture is maintained by a layer of leaves or through shallow insertion into soil from impact, rodent activity, animal trampling, or other soil disturbances. A moisture content of 30 percent or more must be maintained in cool regulated storage to maintain seed viability. Storage conditions have not been determined specifically for Oregon white oak; several methods recommended for keeping seeds moist should be suitable *(46,65)*.

The acorns are large and heavy, averaging about 5 g each (85/lb). Viability has been better than 75 percent in the few samples tested *(46)*, but the usual quality of the seeds is unknown. The seeds are not dormant; they will germinate soon after dispersal if subjected to warm, moist conditions. They will also germinate prematurely in low-temperature stratification. Normally, seeds retain viability only until the next growing season; chances of extending the viability period have not been determined.

Seedlings of Oregon white oak generally appear in the spring. Germination is hypogeal, and the rapid development of a deep taproot is believed responsible for their ability to establish in grass. Shoot development is relatively slow but can be greatly accelerated with long photoperiods *(43)*. Seedlings are not produced now for forest plantings, but raising them in containers is readily possible. Direct seeding of acorns should also prove successful if seeds and young seedlings are protected from rodents and other predators. In at least some circumstances, natural reproduction from seed seems to occur readily *(13,28,35)*.

Vegetative Reproduction—Oregon white oak sprouts abundantly from dormant buds on cut stumps, root collars, and along exposed trunks. Sprouts provide the most certain way to obtain natural regeneration. In 3 years, stump sprouts in 49 clumps in northwestern California averaged 10 per clump; height of the tallest sprout averaged 2.8 m (9.2 ft) and crown diameter per clump 2.5 m (8.2 ft) *(52)*. Larger stumps produced more sprouts, larger clumps, and faster growing shoots. The spread of Oregon white oak by root sprouts has been noted in widely separated instances *(28,68,69,70,71,74)*. In general, the rooting or layering of oak cuttings is difficult, and there is no reason to believe that Oregon white oak would be easier to reproduce by these methods than other oaks.

Sapling and Pole Stages to Maturity

Growth and Yield—Under favorable conditions, mature Oregon white oak trees are 15 to 27 m (50 to 90 ft) tall and 60 to 100 cm (24 to 40 in) in d.b.h. *(34,48,72,73)*. A maximum height of 36.6 m (120 ft), crown spread of 38.4 m (126 ft), and diameter of 246 cm (97 in) at d.b.h. are on record *(2,35)*. Typically, open-grown trees have short boles bearing very large, crooked branches that form dense, rounded crowns (fig. 3). Such trees occupy much space but do not produce much volume for commercial use, except for fuel. In contrast, forest-grown trees 70 to 90 years old have slim, straight boles, fine side branches, and narrow crowns *(60)*. Trees measured in northwestern California had average form classes of 63 and 68 *(34)*. Branchwood of trees over 60 cm (24 in) in d.b.h. averaged 24 percent of total cubic volume. Trees of better form are probably developing now because young stands are more even aged and better stocked than those in the past, but such stands are limited in extent and widely scattered.

Resource inventories of various intensities indicate that the Oregon white oak type occurs on at least 361 400 ha (893,000 acres) in California, Oregon, and Washington and, as a species, comprises 26.2

million m^3 (926 million ft^3) or more of growing stock *(7,8,9,10,21,25,26,27)*. As a component of woodland and other vegetation types, Oregon white oak is found on an additional 299 100 ha (739,000 acres) in California and in sizeable, undefined areas in Oregon and Washington. In California, the mean stand growing-stock volume in the type was 76.9 m^3/ha (1,099 ft^3/acre), and the maximum found was 314.7 m^3/ha (4,498 ft^3/acre).

Oregon white oak generally grows slowly in both height and diameter, but there are exceptions. Limited data from widely separated locations indicate that six to eight rings per centimeter (16 to 20/in) is a common rate for slower growing Oregon white oaks *(28,68,72,75)*. For example, trees in a full stand 47 to 70 years old on deep Willakenzie soil at Corvallis, OR, averaged 14 m (46 ft) in height, 15 cm (6.0 in) in d.b.h., and eight rings per centimeter (20/in) in radial growth *(38)*. Oregon white oak has the capability, however, of growing faster than five rings per centimeter (13/in) *(31,48,72,80)*. In the Cowlitz River Valley, the fastest rate shown on large stumps was 1.9/cm (4.9/in); in the Willamette Valley, the rate averaged 4.6/cm (11.8/in) for four forest-grown trees 95 to 135 years old that averaged 24 m (80 ft) tall and 48 cm (19 in) in d.b.h.

Basal area of Oregon white oak stands has ranged from 8.0 to 60.8 m^2/ha (35 to 265 ft^2/acre), with up to 19.3 m^2/ha (84 ft^2/acre) additional basal area of other species present. In these and other stands averaging 10 cm (4 in) or more in d.b.h., number of oak stems ranged from 10 to 2,800/ha (4 to 1,133/acre) *(1,4,31, 62,69,70,72,75)*. Volumes for stands on different sites and of different ages are not known. One 80-year-old stand that averaged 160 trees 9 cm (3.6 in) and larger in d.b.h. would yield about 94.5 m^3/ha (15 cords/acre) *(60)*.

Rooting Habit—Oregon white oak has a deep taproot and a well-developed lateral system; it is very windfirm even in wet areas. Fast taproot extension and sparse development of laterals are shown by seedlings in the first few weeks of growth. Despite formation of a deep taproot, a high percentage of oak roots are found in upper soil layers. Only 11 percent of the total number of oak roots were found below 76 cm (30 in) in deep Willakenzie soil *(38)*. In contrast, 28 percent of the total Douglas-fir roots in the same soil were found below 76 cm (30 in).

Reaction to Competition—Oregon white oak has been classed as intermediate in tolerance, intolerant, and very intolerant of shade *(47)*. Perhaps such a range of tolerance best describes its status in different situations. Clearly, it is not tolerant of overtopping by Douglas-fir and associated conifers. Dead oaks often found beneath Douglas-fir canopies bear witness that they could not endure the shade *(40,72)*. In some locations and situations, Oregon white oak perpetuates itself, indicating that it can reproduce adequately in its own shade. Branch development on open-grown trees may be very dense. Sparse development of side branches in closed stands provides evidence, however, that it should be classed as intolerant of shade.

Oregon white oak functions as both a seral and a climax species. It is long lived, reproduces from both seeds and sprouts, forms nearly pure stands, and can endure great adversities. In fact, it rates as a climax species because it has greater ability than other species to establish itself and persist where yearly or seasonal precipitation is sparse, where soils are shallow or droughty, or where fire is a repeated natural occurrence.

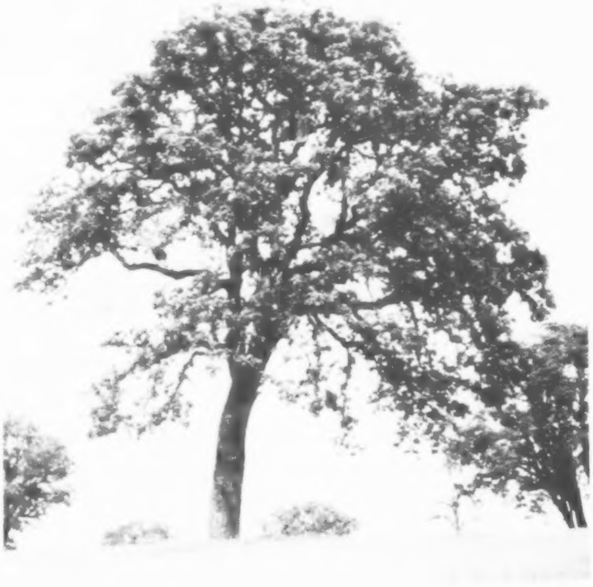

Figure 3—*Mature open-grown Oregon white oak on a cultivated knoll near Amity, OR; its establishment predates settlement of the Willamette Valley.*

Geologic and floristic evidence indicates that Oregon white oak associations have evolved through successive eras as components of relatively arid pine-oak forests, have repeatedly advanced northward from a locus in the southwestern United States and

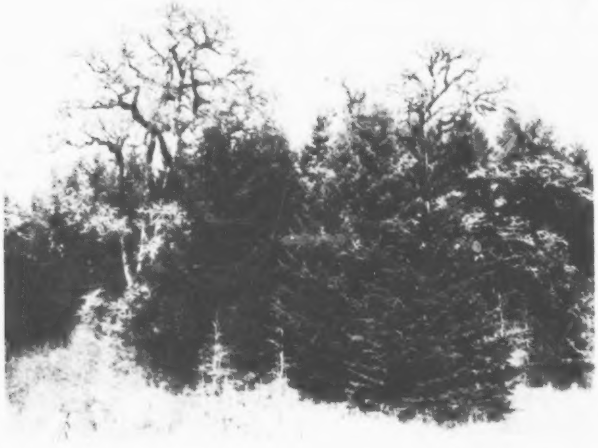

Figure 4—*In the absence of fire, many Oregon white oak stands are invaded and eventually overtopped by Douglas-firs.*

northwestern Mexico, and have repeatedly retreated as North American climates warmed and cooled *(16)*. The most recent northward advance ended about 6,000 years ago; the more arid vegetation types, including oak woodlands, are now being replaced by conifer forest favored by the climatic trend toward cooler and moister conditions.

The seral role of Oregon white oak is illustrated by major changes occurring in the Willamette Valley. Open oak woodlands, savannas dotted with oaks, and grasslands were prominent and widespread before the territory was settled; fires—natural as well as those set by Indians—maintained these open conditions *(30,31,36,44,61)*. Postsettlement exclusion of fire permitted development of closed-canopy white oak stands that are typically of two ages—large spreading trees, now 270 to 330 years old, are scattered among smaller trees of narrow form, 60 to 150 years old *(73)*. Where not restricted by agricultural practices, young oaks continue to encroach into grassland. But, in turn, many oak stands are being invaded and superseded by bigleaf maples or conifers, mainly Douglas-fir (fig. 4). A similar sequence of events is occurring in the northern oak woodland, a distinctive Oregon white oak type in California *(5,51,69)*. Unless steps are taken to reverse present trends, the Oregon white oak type will continue to become a less prominent part of the western flora. A reduction in species diversity will also occur, for open-canopy communities have a more varied composition than closed conifer communities *(13)*.

Damaging Agents—Because of their attractiveness as food, seed crops of Oregon white oak are often decimated quickly *(12)*. Larvae of the filbertworm *(Melissopus latiferreanus)* and the filbert weevil *(Curculio occidentalis)* damage crops even before acorns ripen *(23)*. Maturing or ripe acorns are consumed by woodpeckers, pigeons, doves, jays, wood ducks, mice, chipmunks, squirrels, pocket gophers, woodrats, deer, bear, and other wildlife, as well as by domestic animals.

Wind, wet snow, and freezing rain damage Oregon white oak less than associated hardwoods, but in tests it showed only moderate resistance to cold. Dormant buds collected northwest of Corvallis, OR, withstood -15° C (5° F) and twigs -20° C (-4° F) without injury *(55)*.

Large Oregon white oaks are obviously fire resistant; they have withstood annual or periodic fires for years. But small oaks may be killed or badly damaged by fire, as evidenced by the increased density and spread of oak stands since the advent of fire control.

More than 110 pathogens have been found on the leaves, twigs, trunk, or roots of Oregon white oak *(59)*. Most are of minor consequence; many are saprophytes. Leaf-spot, mildew, and anthracnose fungi sometimes attack the foliage, but control methods have been suggested for only one—an anthracnose disease *(Gnomonia quercina)*. In 1968, this fungus caused moderate to severe dying of leaves and possibly death of oak trees in southern Pierce County, WA *(14)*. Premature browning of foliage is occasionally widespread in the Willamette Valley, but the causes and effects have received only incidental attention. The hairy mistletoe is common on Oregon white oak in Oregon and California, forming conspicuous, rounded growths in the upper crown (fig. 2). Its effect on growth and vigor of this host is undetermined. The white pocket root and butt rot *(Polyporus dryophilus)* and the shoestring root rot *(Armillaria mellea)* are probably the most damaging rots found in Oregon white oak. Its heartwood is generally very durable; stumps and even relatively small stems may remain intact for years.

Although Oregon white oak is host to hundreds of insect species *(19)*, damage is usually not severe, and loss of trees to insect attack is uncommon. The western oak looper *(Lambdina fiscellaria somniaria)* is probably the most damaging insect on white oak from Oregon north to British Columbia. In some years, oaks over large areas in the Willamette Valley are defoliated *(23)*. The damage is temporary since the trees leaf out the next year and outbreaks are not sustained. The western tent caterpillar *(Malacosoma californicum)* and the Pacific tent caterpillar (*M. constrictum*) are widely distributed defoliators with a preference for oaks. Several species of aphid, particularly *Tuberculatus columbiae*, feed on the underside of oak leaves; the snowy tree cricket (*Oecanthus fultoni*) lives in open-grown oaks and associated species; and several leafrollers (*Abebaea cervella* and *Pandemis cerasana*) are found on Oregon white oak. Oregon white oak is the principal host for *P. cerasana*, an introduced leafroller causing sporadic defoliation that is now maintaining a relatively high population and slowly extending its range around Victoria, BC (*17*). Many gall wasps are found on oaks; those prominent on Oregon white oak include *Andricus californicus*, which forms large, persistent, applelike galls on twigs; *Bassettia ligni*, which causes seedlike galls under the bark of branches that often girdle and kill the branch; *Besbicus mirabilis*, which forms mottled, spherical galls on the underside of leaves; and *Neuroterus saltatorius*, which forms mustard-seed-like galls on lower leaf surfaces that drop in the fall and jump around like Mexican jumping beans caused by activity of the enclosed larvae (*18,23*).

Only incidental damage by animals has been noted on vegetative parts of Oregon white oak. Douglas squirrels and western gray squirrels sometimes debark small branches infested by gall wasp larvae (*64*). Damage is scattered and may involve as much as one-fourth of a tree's crown. Gophers and other burrowing animals, which are abundant on forest borders, damage some roots. Livestock inflict some trampling and feeding damage on young oaks.

Special Uses

The wood of Oregon white oak is dense, with specific gravity ranging from 0.52 to 0.88 when ovendry (*66*), has moderate strength in static bending tests, but does not absorb shocks well (*47*). It rates high in compression and shear strength and is outstanding among 20 northwestern woods in tension and side hardness tests (*47*). The heartwood is at least as durable as that of white oak (*Quercus alba*) (*58*). Pallets made from Oregon white oak compare favorably in strength with those made from other species (*66*) and are higher in withdrawal resistance for nails or staples (*41*).

Specialty items, fenceposts, and fuel are now the primary uses of Oregon white oak. The wood is considered one of the best fuels for home heating and commands top prices. It has been used for flooring, interior finish, furniture, cooperage staves, cabinet stock, insulator pins, woodenware, novelties, baskets, handle stock, felling wedges, agricultural implements, vehicles, and ship construction (*60*). Consumption of Oregon white oak totaled 12 454 m^3 (2,185,000 fbm) exclusive of fuel in 1910 but has since declined (*60*).

Although Oregon white oak is not grown commercially for landscape purposes, scattered native trees, groves, and open stands are highly valued scenic assets in wildland, farm, park, and urban areas (*35,42,49,56*). Mistletoe is a scenic growth on Oregon white oaks that is collected and sold as a decorative and festive minor product.

Until recent times, meal or mush made from acorns of many oaks (including Oregon white oak) was a common Indian food (*35,71,81*). When crops were heavy, white oak acorns were also gathered and stored by local ranchers for feed, mainly for hogs. Livestock forage for acorns and prefer those of white oaks to black oaks (*81*). The leaves have a protein content of 5 to 14 percent (*35,56*), and Oregon white oak is rated as good to fair browse for deer but poor for domestic livestock.

Oregon white oak woodlands and forests provide favorable habitat for wildlife (*6*) and also produce substantial amounts of forage for sheep and cattle (*33*). Infrequently, cattle are poisoned by foraging on oak; one instance involving Oregon white oak has been documented (*37*).

Oak-dominated forests in the western part of the Willamette Valley in Oregon have a higher diversity of birds in all seasons than adjacent conifer forests (*3*). Oregon white oak and ponderosa pine—Oregon white oak associations are preferred brood habitats for Merriam's wild turkey in south-central Washington (*39*).

Greenhouse experiments have shown that Oregon white oak is a good host for the gourmet truffle, *Tuber melanosporum* (*43*). The feasibility of managing Oregon white oak stands for truffle production, as many oak stands are managed in Europe, is being investigated.

Genetics

Though Oregon white oak populations in Washington are disjunct and scattered, the chemical and morphological characteristics of their foliage are similar (*71*). Genetic differences appear so minor that seed distribution from a common source by Indians has been postulated. Ecotypic variation was observed in top and root growth of young seedlings from seed collections made from Corvallis, OR, southward (*43*). First-year seedlings from northern sources were taller and heavier.

Quercus garryana hybridizes naturally with four other oaks. *Quercus* × *subconvexa* Tucker (*Q. durata* × *garryana*), a small tree found in Santa Clara and Marin Counties, CA, is noteworthy because of its morphologically dissimilar parents—*Q. garryana* is a deciduous tree, *Q. durata* an evergreen shrub, and the hybrid is tardily deciduous *(74)*. *Quercus* × *howellii* Tucker *(Q. dumosa* × *garryana)* is also a small tree found in Marin County and a hybrid between a deciduous tree and an evergreen or tardily deciduous shrub or tree. *Quercus* × *eplingii* C. H. Muller *(Q. douglasii* × *garryana)*, a tree with deciduous leaves, is found in Lake and Sonoma Counties, CA *(75)*. Hybrids between *Q. garryana* and *Q. lobata* are also found in Sonoma County *(4)*.

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Quercus kelloggii Newb. California Black Oak

Fagaceae Beech family

Philip M. McDonald

California black oak *(Quercus kelloggii)* exceeds all other California oaks in volume, distribution, and altitudinal range. Yet this deciduous hardwood has had little sustained commercial use and almost no management, even though its wood closely resembles that of its valuable, managed, and heavily used counterpart—northern red oak *(Quercus rubra)*—in the Eastern United States.

First collected in 1846 near Sonoma, CA, the species was not named until 1857 when John Newberry called it *kelloggii* in honor of Albert Kellogg, a pioneer California botanist and physician *(17)*. In later botanical works, the species was called *Q. californica* and black oak or Kellogg's oak.

Acorns of California black oak were carried from San Francisco to England in 1878. Thirty-two years later, trees from these acorns were described as being 30 feet tall and making good growth *(10)*.

Habitat

Native Range

The north-south range of California black oak (fig. 1) is about 1255 km (780 mi). In Oregon, its natural range extends from just north of Eugene, southward through the valleys west of the Cascade Range. The species is especially frequent along lower slopes in fairly dry sections of the Klamath and Cascade Mountains but never grows near the Pacific Ocean. In California, black oak is found in the northern Coast Range from the Oregon State line to Marin County and then intermittently in the Santa Cruz and Santa Lucia Mountains. This oak becomes more common on the San Bernardino, San Jacinto, and Agua Tibia Mountains, extending to just south of Mt. Laguna, and is now recognized as being in Baja California (5). In California's Sierra Nevada, the species grows abundantly along the west side, from near Lassen Peak to near Kings Canyon. California black oak becomes intermittent southward to the Tehachapi Mountains, where it again increases in abundance. California black oak is generally confined to the westside, but a few stands have been found along the eastside of the Sierra Nevada. The species approaches the Nevada State line northeast of Beckwourth Pass but is not reported in Nevada.

Climate

Hot dry summers and cool moist winters characterize the climate where California black oak grows. Within the species' natural range, average annual precipitation varies widely. In the valleys of southwestern Oregon, it exceeds 760 mm (30 in); in northwestern California, it ranges from 760 to 2540 mm (30 to 100 in); and in northeastern California, only 300 to 380 mm (12 to 15 in) of rainfall annually. Throughout the range of black oak in north-central and central California, annual precipitation averages 1010 to 1780 mm (40 to 70 in) but may exceed 2920 mm (115 in) locally. In these areas less than 4 percent of the yearly precipitation falls from June through September. In the mountains of southern California, precipitation averages 910 mm (36 in). Black oak achieves its best size and abundance in areas where snowfall accounts for 10 to 50 percent of the year's precipitation.

Average mean daily temperatures range from -1° to 8° C (31° to 46° F) during January, and from 19° to 28° C (66° to 82° F) in July. The last killing spring frost is expected between March 15 and June 9, and the first killing frost in the fall between August 30 and November 30. Periods free of killing frosts range from 82 to 270 days. Throughout an 18-year period, the highest temperature recorded at 1125 m (3,700 ft) elevation in the center of black oak's zone of greatest size and abundance was 39° C (103° F); the minimum temperature was -15° C (5° F). The maximum number of frost-free days was 215 and the minimum was 116 *(35)*.

Soils and Topography

Probably the most important single soil variable that limits the presence of California black oak is internal drainage. Black oak is not found growing "with its feet wet." The species is adapted to soils derived from diverse parent materials—andesite, basalt, granite, pumice, quartz diorite, sandstone, schist, shale, and volcanic tuffs and breccias. California black oak only rarely is found on soils originating from serpentine. Occasionally it grows on soils derived from ultrabasic parent material, but mostly where above-average amounts of calcium seem to offset the deleterious effects of magnesium.

Soil textures favoring this oak range from medium-textured loams and clay-loams to the more coarse-textured gravelly-clay-loams and sandy-loams. In-

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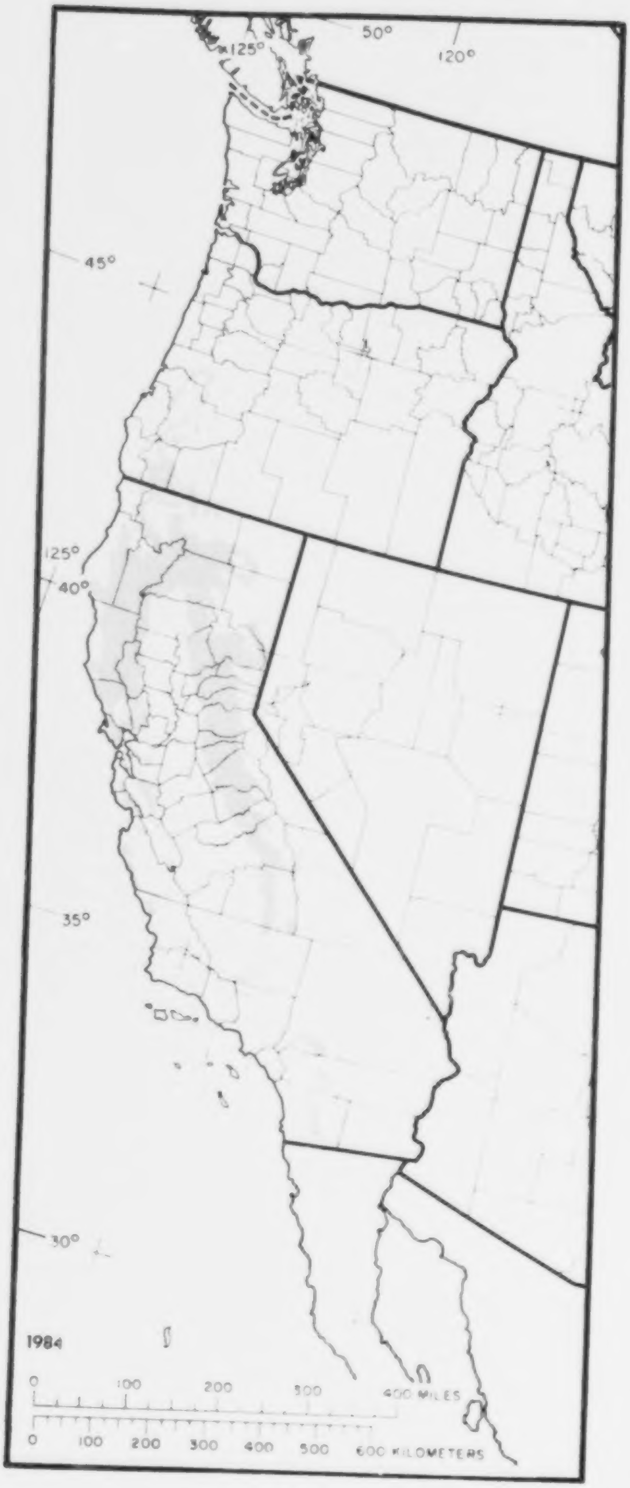

Figure 1—*Native range of California black oak.*

creasing clay content in the surface soil usually means a decreasing incidence of black oak. In fact, this species rarely is found on soils with clay topsoils, particularly if the clay is heavy and sticky. Black oak usually grows on thin soils and rocky slopes, but always at the cost of abundance or form, or both. In general, black oak grows best on medium- to coarse-textured, deep, and well-drained soils.

About 75 soil series in California have been identified by the California Cooperative Soil-Vegetation Survey and the National Cooperative Soil Survey as supporting California black oak. Important soil series in the California Coast Range include Boomer, Cohasset, Josephine, Sites, and Sheridan. In the Sierra Nevada, Aiken, Chawanakee, Holland, Stump Springs, Corbett, and Tish Tang support abundant black oak. Soils in the southern Cascade and Klamath Mountains that often are clothed with black oak include Aiken, Cohasset, McCarthy, Sites, Tournquist, Behemotosh, Horseshoe, and Neuns. Fourteen soil series have been identified in Oregon, mostly on series similar to those in California. Most of the soils in both States are found at higher elevations and support forest vegetation rather than oak woodland or chaparral. Soil orders are mostly Alfisols and Inceptisols, occasionally Mollisols.

The best black oak stands in the Coast Range and Klamath Mountains are found on deep, slightly acid loams and gravelly-clay-loams derived from sandstone and shale. In the southern Cascade Range and northern Sierra Nevada, black oak grows best on deep loams and clay-loams originating from metavolcanic rocks. In the central and southern Sierra Nevada and in the Transverse and Peninsular Ranges, this oak grows well on deep, acid to moderately acid sandy-loam soils derived from granitic rock.

California black oak grows within a wide elevational range—from the level gravelly floors of low valleys to alluvial slopes, rocky ridges, and high plateaus. Most of the terrain is rugged, steep, and dissected by major streams and ephemeral drainages.

In Oregon, the elevational range of black oak varies from 137 m (450 ft) near Eugene, to more than 305 m (1,000 ft) on the low rounded hills in the Umpqua River drainage *(13)*. The oak also is found within this elevational range on the eastern slopes of the Coast Range and the western slopes of the Cascades. In south central Oregon and the Klamath Mountains, black oak grows at higher elevations of 610 to 915 m (2,000 to 3,000 ft).

In California's Coast Range, black oak is found from about 152 m (500 ft) along the Mattole River in Humboldt County to 1830 m (6,000 ft) in the Yolla Bolly Mountains. Black oak reaches its lowest elevation (60 m or 200 ft) in the Napa and Santa Rosa Valleys. Most black oak in the central portion of the Coast Range grows between 305 to 1525 m (1,000 to 5,000 ft), gradually increasing in elevation but narrowing in range to 1220 to 1982 m (4,000 to 6,500 ft) in Santa Barbara and eastern Ventura Counties. Farther south in the Transverse Range the species is found at elevations of 1403 to 2135 m (4,600 to 7,000 ft) *(39)*. In the San Jacinto Mountains, black oak reaches 2440 m (8,000 ft) and, at its southernmost extension in the Peninsular Range of San Diego County, it grows within the 1525- to 1830-m (5,000- to 6,000-ft) elevation.

The elevational range of black oak in California's Cascade Range is from about 183 m (600 ft) in western Shasta County to 1906 m (6,250 ft) in south-central Shasta County. In the Sierra Nevada, lower elevational limits for black oak range from 458 m (1,500 ft) in the north to 1220 m (4,000 ft) in the south. Upper limits increase north to south from about 1982 to 2380 m (6,500 to 7,800 ft).

California black oak is most abundant and attains its largest size in the Sierra Nevada. Extensive stands of excellent development also are found in eastern Mendocino and Humboldt Counties of the north Coast Range. Elevation and aspect often interact to govern abundance and development. At elevations below 305 m (1,000 ft) in north-central California, black oak is found primarily in sheltered draws or on north slopes. With increasing elevation, favorable aspects increase until at 762 to 915 m (2,500 to 3,000 ft) all aspects support California black oak, providing soil is deep enough. Above 1067 m (3,500 ft), north- and east-facing slopes often are devoid of black oak, although other vegetation grows well. In the southernmost mountains, black oak is found on west-facing slopes, but only where soils are deep, temperatures are cool, and soil moisture is adequate.

Associated Forest Cover

California black oak is a component of six forest cover types *(11)*. It is the prime constituent of California Black Oak (Society of American Foresters Type 246) and a major component in two others: Douglas-Fir–Tanoak–Pacific Madrone (Type 234) and Pacific Ponderosa Pine–Douglas-Fir (Type 244). Black oak becomes important in Sierra Nevada Mixed Conifer (Type 243) and Pacific Ponderosa Pine (Type 245) after severe disturbance or fire. The oak is a minor component in Canyon Live Oak (Type 249).

The successional status of California black oak is not clear. It has been implied that the species was climax because the type in which it was a part represented a degree of mesophytism between that of the chaparral and the conifer forest *(7)*. The species was also thought to be more a persistent subclimax than climax.

California black oak, or its fossilized equivalent (*Quercus pseudolyrata*), was much more widespread in past ages than now. Fossil remains indicate that the species was abundant in sedimentary deposits near Spokane and Ellensburg, WA, in the John Day Valley and Blue Mountains of Oregon, and in northwestern Nevada *(6)*. These deposits date back to the Miocene epoch of 12 to 26 million years ago. Increasing aridity is the probable cause for the smaller natural range of black oak today.

The most common botanical associate of black oak is ponderosa pine (*Pinus ponderosa* var. *ponderosa*). The two species intermingle over vast acreages, except that black oak is found at lower elevations, on sites too poor to support pine, and in certain areas within the redwood region of California where pine does not grow. Another exception is that this oak is rarely found in Interior Ponderosa Pine (Type 237) *(11)*. In California and Oregon, therefore, where the natural ranges of the two species coincide, ponderosa pine sites generally are fertile ground for black oak. And black oak sites are almost always fertile ground for ponderosa pine.

At lower elevations, black oak often serves as a nurse tree to conifers. Ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and incense-cedar (*Libocedrus decurrens*) seedlings often become established beneath the sheltering crowns of large black oaks while adjacent ground remains bare *(2)*.

A rule-of-thumb is that black oak never grows through a stand of ponderosa pine but can grow through brush *(9)*. Without disturbance, black oak is eventually crowded out of the best sites and remains only as scattered remnants in mixed-conifer forests. Here it often exists on "islands" of soil or terrain not favorable for natural regeneration of conifers.

Black oak grows individually or in groves, some of which are quite extensive. Usually each grove is of one age-class, the result of sprouting after fire *(34)*. Rarely does it exist as an understory, especially beneath a closed canopy. The species is usually a component of hardwood stands or of mixed hardwood and conifer forests. Tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) are the most common hardwood associates of black oak. Other hardwood associates at lower elevations are Oregon white oak (*Quercus garryana*), interior live oak (*Q. wislizenii*), coast live oak (*Q. agrifolia*), Engelmann oak (*Q. engelmannii*), and blue oak (*Q. douglasii*). At higher elevations Pacific dogwood (*Cornus nuttallii*), bigleaf maple (*Acer macrophyllum*),

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California-laurel (*Umbellularia californica*), and canyon live oak (*Quercus chrysolepis*) intermix with California black oak.

Besides ponderosa pine, conifer associates at low elevations are knobcone pine (*Pinus attenuata*), Monterey pine (*P. radiata*), Digger pine (*P. sabiniana*), and redwood (*Sequoia sempervirens*). At intermediate elevations within the natural range of California black oak are California white fir (*Abies concolor* var. *lowiana*), grand fir (*A. grandis*), incense-cedar, Coulter pine (*Pinus coulteri*), sugar pine (*P. lambertiana*), giant sequoia (*Sequoiadendron giganteum*), Douglas-fir, California torreya (*Torreya californica*), and bigcone Douglas-fir (*Pseudotsuga macrocarpa*). At higher elevations black oak intermingles with western juniper (*Juniperus occidentalis*) and Jeffrey pine (*Pinus jeffreyi*).

Shrub associates include at least 30 species, some of the most important of which are greenleaf manzanita (*Arctostaphylos patula*), whiteleaf manzanita (*A. viscida*), deerbrush (*Ceanothus integerrimus*), bear-clover (*Chamaebatia foliolosa*), oceanspray (*Holodiscus discolor*), Brewer oak (*Quercus garryana* var. *breweri*), Sierra coffeeberry (*Rhamnus rubra*), Sierra gooseberry (*Ribes roezlii*), and poison-oak (*Toxicodendron diversilobum*). In parts of Shasta and Trinity Counties, and perhaps elsewhere, black oak itself takes a shrub form. The stands so formed usually are dense and tangled—ideal habitat for deer and upland game.

Except on the fringe of black oak's natural range, especially at the lowermost elevations, most shrubs generally are not competitive, nor particularly abundant over most of the forest land where black oak grows. After heavy cutting or fire, however, some of the more aggressive shrubs often compete strongly with black oak sprouts.

When compared with 15 of its most common shrub associates in the Klamath Mountains of northern California, black oak ranked ninth in need of soil moisture, third in demand on soil nutrients, eighth in terms of tolerance, and first in rapidity of sprouting (*32*). The species is able to withstand high moisture stress (*37*) and to become established and grow well on harsh sites where few other species are capable.

Life History

Reproduction and Early Growth

Flowering and Fruiting—California black oak flowers from mid-March to mid-May depending on elevation, physiography, and local climatic conditions. In general, trees near the coast and at lower elevations bloom earliest.

Flowers on black oak are unisexual. The plant is monoecious. Staminate flowers are long (3.5 to 7.5 cm or 1.4 to 3.0 in) hairy aments that emerge from buds in the leaf axils of the previous year's growth. The five to nine stamens in each ament have bright red anthers and pale green filaments. The calyx is light green. Pistillate flowers are borne singly or two to seven on a short stalk that originates from leaf axils of the current year's growth. The stigmas are dark red.

Acorns mature in the second year. Early in the second summer the immature acorn resembles a small globe about 6 mm (0.2 in) in diameter. At this stage, the acorn is completely encapsulated in the cup. At maturity the light brown, thin-scaled cup encloses from 0.5 to 0.75 of the acorn. Acorns form singly, or in clusters of two to six, and vary widely in dimension. Sizes range from 1.9 to 4.4 cm (0.7 to 1.7 in) long and from 0.9 to 3.8 cm (0.4 to 1.5 in) in diameter.

Seed Production and Dissemination—In natural stands, black oak must be 30 years or older before it produces viable seed. The oak produces some acorns sporadically between ages 30 and 75, but seldom large quantities before 80 to 100 years. A few trees bear at least some acorns every year. Others of similar diameter and crown characteristics rarely produce acorns. Trees that are good seed producers continue abundant acorn production at least to 200 years.

Age, diameter of bole, and crown width influence acorn yield (*22*). A general relationship for a medium seed crop on a good forest site is that acorn yield increases as bole and crown diameter increase, at least through age 200:

Age	Bole diameter		Crown diameter		Acorn yield	
yr	*cm*	*in*	*m*	*ft*	*kg*	*lb*
30	13	5	5	15	0	0
50	23	9	6	20	2	5
80	33	13	8	26	9	20
100	43	17	10	32	27	60
150	61	24	12	41	45	100
200	81	32	16	52	64	140

Estimates of acorn production by tree or size of seed crop are scarce. One large, 150- to 200-year-old black oak in Butte County, CA, produced about 6,500 acorns for a crop year rated as fair. Acorns were large and heavy, numbering 115/kg (52/lb). Black oak acorns usually are smaller, numbering between 115 and 324/kg (52 and 147/lb). Large acorns have been observed at both low and high elevations and small acorns at medium elevations. The factors influencing acorn size probably are many, but little is known about their interaction. A single, large, well-developed tree at a low elevation in Shasta County, CA, produced sound acorns each year as follows:

1974	700
1975	1,000
1976	65
1977	0
1978	320
1979	231
1980	125

The magnitude and periodicity of seed crops appear to be quite variable. One study reported that abundant seed crops for entire stands were produced at 2- to 3-year intervals *(31)*. At 760 m (2,500 ft) elevation in Yuba County, CA, medium to bumper seed crops were produced in 4 of 20 years. At 850 m (2,800 ft) elevation in south-central Shasta County, medium to bumper crops were borne on large black oaks in 4 of 8 years. At a lower elevation in Shasta County (170 m or 560 ft), black oaks yielded sound acorns in 6 of 7 years. Of these, two each rated as bumper, medium, and light.

Insects destroy many acorns, primarily in the developmental stage. Immature acorns are attacked by both lepidopterous and coleopterous pests. The filbertworm (*Melissopus latiferreanus*) and the filbert weevil (*Curculio uniformis*) are particularly destructive, in some places infesting up to 95 percent of the acorns and destroying most of a crop *(16)*. Fire may lessen these losses. On the Shasta-Trinity National Forests in California, a prescribed burn in March 1978 resulted in a bumper crop of sound black oak acorns, while trees on unburned ground nearby bore only unsound acorns. Apparently, destructive insects in the duff and soil were reduced greatly by the fire *(33)*.

Fully developed acorns begin falling in mid-August at lower elevations, and in mid-September at higher elevations. Almost all acorns that fall first are hollow or infested with insects. Some are still green or greenish yellow. Sound acorns begin dropping from late September to early November and cease by November 15 at lower elevations. At higher elevations almost all acorns have fallen by early December.

Acorns generally drop just before or during leaf fall. Once on the ground, temperature can be critical to continued viability, and fallen leaves help keep acorn temperatures below lethal thresholds. In one instance, fully mature acorns exposed to the hot fall sun had withered cotyledons after 9 days. Acorns from the same trees showed full-sized cotyledons after 21 days, if protected by leaves and branches *(21)*. Likewise, cotyledons of acorns exposed to freezing temperatures turned gray and flaccid, although cotyledons of acorns beneath tree crowns and covered with leaves remained white, crisp, and firm.

A blue-gray mold also damages fallen seed. At one location, acorns covered for about 2 months by wet leaves showed mold at the blunt ends that had progressed well within the seeds. For other acorns in this same environment, cutting tests showed that cotyledons were unaffected. American Indians, however, gathered only freshly fallen acorns to avoid the mold *(15)*.

Because the acorns are large and heavy, most fall directly beneath tree crowns. Few bounce or roll far on steep slopes covered by duff, leaves, and litter. Animals play a vital role in dissemination of acorns because they transport some of them away from the parent tree. The western gray squirrel and the scrub jay are the most important disseminators, for they bury the acorns, sometimes spreading the species to areas nearby.

Black oak acorns are eaten by at least 14 species of song and game birds, many species and subspecies of small mammals (mostly rodents), and mule deer *(20)*. Black bears in the San Bernardino Mountains of southern California utilize the California black oak type in spring, summer, and fall *(28)*. For many of these creatures, acorns are the primary foodstuff in the fall. Without acorns, populations are affected. Fawn survival rates, for example, increase and decrease with the size of the acorn crop.

Cattle, and, to a lesser extent, sheep, also consume many black oak acorns each year.

Seedling Development—California black oak reproduces from seed, but natural regeneration tends to be scanty, poorly distributed, and uncertain. The most likely place to find black oak seedlings is beneath large parent trees, where they number up to 45/m^2 (4/ft^2).

Before the seeds begin to germinate, a period of after-ripening to overcome dormancy is required. Overwintering beneath the litter on the forest floor normally breaks dormancy under natural conditions. For artificial regeneration, acorns can be stratified by cold storage in sealed polyethylene bags thick enough to inhibit moisture loss, but porous enough to freely emit respiration byproducts. Storage temper-ature should be just above freezing and moisture content of acorns maintained at a level where cotyledons are turgid or slightly flaccid, but not dried out.

Natural seedbed requirements for germination are not exacting. Either undisturbed leaflitter or, to a lesser extent, moist, well-aerated mineral soil are good seedbeds. Establishment of black oak is almost nonexistent on heavy clay soils or soils compacted by logging machinery. These conditions reduce the ability of the radicle to penetrate the soil far enough and fast enough to avoid searing soil surface temperatures or the seasonal drying of upper soil layers.

Acorns germinate in the spring when the weather warms. Germination is hypogeal and highly variable, both in magnitude and timing. The radicle is first to emerge and grows downward for some time, often 10 to 20 days, before the epicotyl appears above ground. This process benefits the seedling in getting to and staying in available soil moisture, and in minimizing transpirational losses. Sometimes a single acorn may put forth several epicotyls, particularly if upward progress is hampered by a stony or crusty soil.

Under optimum conditions, 15 to 25 days elapse between sowing of stratified acorns and the beginning of germination. In nature, the germination period may be several weeks or even months. Germinative capacity varies considerably and changes with degree of insect infestation, amount of mold, and depth of acorn in soil, among other variables. Germination has been reported as high as 95 percent and also as scanty (21 percent). Germinative capacities in large-scale field tests in the northern Sierra Nevada were 31 and 38 percent *(22)*.

Black oak seedlings often reach heights of 10 to 15 cm (4 to 6 in) and extend their taproots downward as deep as 76 cm (30 in) in the first growing season. Development of a deep-thrusting vertical root is necessary for seedlings to cope with the hot dry summers characteristic of California black oak's range. For the first few years, therefore, both lateral root development and shoot growth are slow. Shoot growth probably does not begin to accelerate until root capacity is extensive enough to obtain adequate moisture. This may take 6 or 7 years or longer. Shoot growth of some seedlings, particularly those stressed by competing vegetation, never accelerates and these seedlings eventually die.

Studies evaluating artificially regenerated California black oak on the Plumas and Angeles National Forests in California indicate that artificial regeneration of black oak is possible, providing that competing vegetation and pocket gophers are controlled. Fall planting of 1-year-old seedlings, without artificial watering, resulted in good survival and growth on the San Bernardino National Forest, California *(30)*.

Fertilization appears to be one technique for enlarging root capacity and stimulating height development of seedlings. In a test in the northern Sierra Nevada, fertilized seedlings were more than three times taller than unfertilized seedlings (0.2 as against 0.8 m or 0.7 as against 2.5 ft) after five growing seasons. Fertilizer in the proportion of 16-20-0 for nitrogen, phosphorus, and potassium was applied at about 0.1 kg (0.25 lb) per seedling early in the spring of each year *(22)*.

Young black oak seedlings are killed mostly by drought and pocket gophers. Grasshoppers and other insects damage young seedlings, and freezing by late spring frosts injures them. These injuries usually are mitigated by sprouting from the root crown.

Vegetative Reproduction—California black oak sprouts profusely after trees are cut or burned. Most sprouts develop from latent buds, which lie under the bark at, or slightly above, the root collar. Other sprouts originate from the top of the stump or between the top and the ground. These are called stool sprouts and are undesirable for two reasons. They are weakly attached to the parent stump and frequently broken off by wind and snow, and are prone to heart rot at an early age.

The size and vigor of the parent tree determine the number of sprouts and their height and crown spread. In general, stumps from larger trees produce a larger number of sprouts and more vigorous ones. Only old, moribund trees fail to produce sprouts after cutting.

Low stumps of nearly all diameters produce many more sprouts than high stumps. High-stumping an older, larger tree yields undesirable stool sprouts, and often no sprouts from below ground.

Root crown sprouts grow vigorously, especially in full sunlight. Forty-nine stumps were studied in stands on a good site in the northern Sierra Nevada. Sprout density, height, and crown width were evaluated in clearcuttings and in shelterwood stands where 50 percent of the basal area had been removed *(22)*. Number of sprouts, crown width, and especially height growth were consistently greater in the clearcuttings (table 1).

The environment typical of shelterwood cuttings apparently is more favorable to a cynipid gall wasp *(Callirhytis perdens)* than that in clearcuttings. Damage to terminal shoots by this pest is greater under shelterwood stands, accounting in part for the poorer height growth of sprouts. Thinning sprouts to three or four per stump at age 4 showed no gain in height but resulted in undesirable damage to the bole from sunscald and increased forking of stems *(22)*.

Young black oak sprouts grow faster in height than other vegetation, including coniferous associates. Consequently, they remain dominant for many years. Although black oak seedlings extend the species into new areas, sprouts keep the oak in the same area and are responsible for regenerating many more stands than seedlings. Only after the living crown has moved considerably up the bole does black oak begin its role as a nurse tree, aiding conifers to become established and grow to equal or dominant positions in the stand.

Propagation by layering, rooting of cuttings, or grafting has not been reported. But the wartime shortage of cork in the 1940's stimulated grafting of cork oak (*Quercus suber*) to black oak stocks. In a greenhouse trial, 70 percent of the grafts were successful *(27)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Because fire incidence throughout its natural range is high, nearly all black oak trees originated from sprouts. Consequently most California black oak stands are even-aged.

Number of sprouts per stump influences growth, form and, eventually, yield. The number per clump decreases rapidly with age. By the time the sprouts are pole-size, competition within individual clumps has reduced them to two or three, or occasionally, four stems. By age 100, only one or two stems remain. These data are based on 180 clumps at many California sites *(21)*.

The form of California black oak varies greatly. On the fringe of its range and on marginal sites, black oak trees assume a scrubby form. In closed stands on good sites, the oaks tend to be tall and straight with clear boles and thin crowns. When open-grown, black oaks generally fork repeatedly, becoming multi-stemmed and broad-crowned.

The general age-height relationship of California black oak, based on 393 dominant trees in northern and central California, is curvilinear until age 140. Thereafter, tree height remains constant regardless of age. Selected age-heights are 20 years, 8 m (26 ft); 40 years, 13 m (43 ft); 60 years, 17 m (56 ft); 100 years, 22 m (72 ft); and 140 years, 25 m (82 ft) *(21)*.

Position on long continuous slopes also influences growth and form. Trees at the toe of slopes or on gently sloping benches, where deeper soils are likely, generally grow best and have good form. Those at midslope are shorter and more scrubby. On upper slopes, trees grow slowly and are even shorter. Aspect also influences growth. Of the 393 trees noted earlier, 100-year-old trees averaged about 26 m (85 ft) in height on east aspects; 22 m (72 ft) on north aspects; 21 m (68 ft) on west; and 17 m (56 ft) in height on south aspects.

Average site index at base age 50 years is about 15 m (50 ft); better than average, about 18 m (60 ft); and poor, only 11 to 12 m (35 to 40 ft) *(29)*.

Diameter growth is often slow during the first 25 years of a black oak's life. Competition for position in the canopy tends to favor height growth over diameter growth. At 25 years, the average tree is nearly 11 m (35 ft) tall and about 10 cm (4 in) in d.b.h. and is one of three sprouts in the clump. Black oak grows fastest in diameter from age 25 to 65 (table 2). Its growth can reach one ring per centimeter or three rings per inch. At age 65 the tree is about 29 cm (11.5 in) in d.b.h. and has grown almost 0.5 cm/yr (0.2 in/yr).

Table 1—Development of California black oak stump sprouts in a northern Sierra Nevada forest 10 years after cutting

Year after cutting	Sprouts per stump		Height		Crown width	
	Clear-cut	Shelter-wood	Clear-cut	Shelter-wood	Clear-cut	Shelter-wood
	no.		*m*			
0	55+	28	—	—	—	—
2	55+	23	1.2	0.9	1.2	0.7
4	35	17	2.4	1.2	1.8	1.0
6	23	15	3.7	1.5	2.3	1.2
8	18	13	4.9	1.8	2.6	1.6
10	15	12	6.0	2.1	2.9	2.2
	no.		*ft*			
0	55+	28	—	—	—	—
2	55+	23	4	3	4	2
4	35	17	8	4	6	3
6	23	15	12	5	8	4
8	18	13	16	6	9	5
10	15	12	20	7	10	7

Black oak in an understocked stand averages 33 to 35 cm (13 to 14 in) in d.b.h. at 65 years; in an overstocked stand, it averages between 18 and 23 cm (7 to 9 in). After age 65, diameter growth slowly declines. By age 90 most trees are mature.

Diameter growth of California black oak can be increased greatly by thinning. On a good site in the northern Sierra Nevada, diameter growth rates of trees thinned when 60 years old were twice that of unthinned trees of similar age 8 years after thinning *(23)*.

Black oak may live to be almost 500 years old, but age-diameter relationships beyond 120 years are uncertain. Trees 51 cm (20 in) in d.b.h. can range between 70 and 175 years. Trees 41 to 63 cm (16 to 25 in) in d.b.h. were 175 to 275 years old, and those more than 102 cm (40 in) were 175 to 325 years old (fig. 2).

Black oak seldom exceeds 1.5 m (5 ft) in d.b.h. or 40 m (130 ft) in height. The largest living black oak

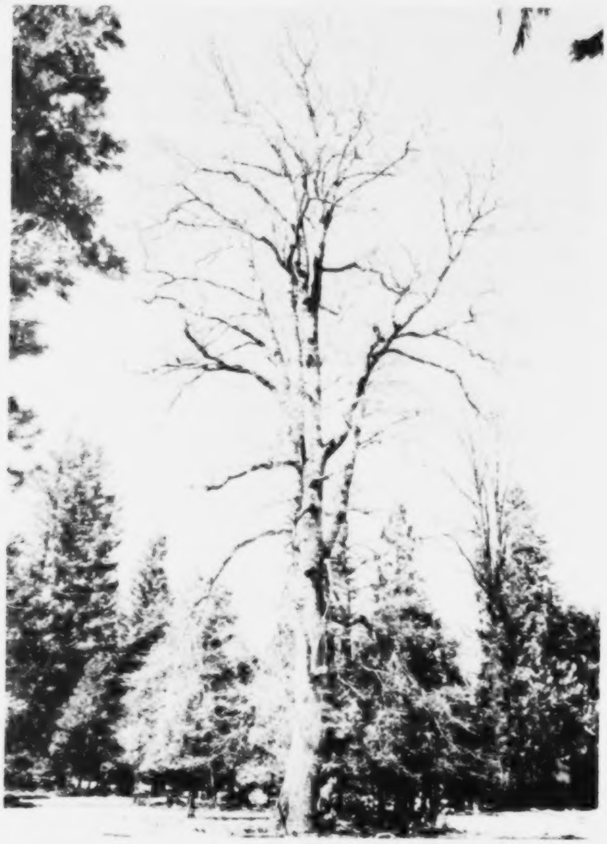

Figure 2—*California black oak near Shingletown, Shasta County, CA; it is nearly 37 m (121 ft) tall, 159 cm (63 in) in d.b.h., and 180 years old.*

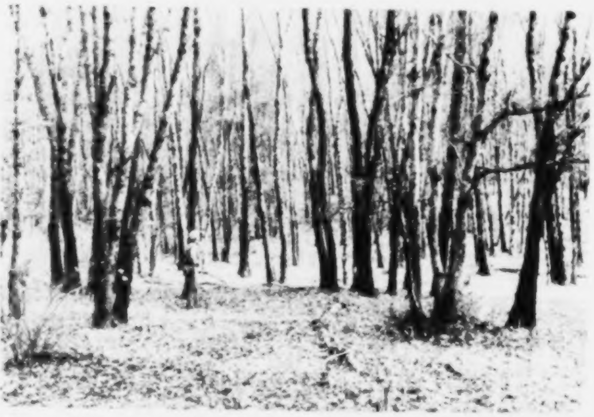

Figure 3—*Interior view of a natural 70-year-old California black oak stand of average stocking, density, and growth rate. Trees average 30 cm (12 in) in d.b.h. and more than 18 m (60 ft) in height.*

Table 2—Diameter growth in natural stands, California black oak, 1968[1]

Age	D.b.h.		Average cumulative increment per decade	
yr	*cm*	*in*	*cm*	*in*
20	9	3.4	4.32	1.70
30	14	5.4	4.57	1.80
40	18	7.2	4.57	1.80
50	23	9.0	4.57	1.80
60	27	10.8	4.57	1.80
70	31	12.2	4.42	1.74
80	34	13.4	4.27	1.68
90	37	14.6	4.11	1.62
100	40	15.6	3.96	1.56
110	42	16.6	3.84	1.51
120	44	17.5	3.71	1.46

[1] Basis: 405 dominant trees in 45 even-aged stands, many California sites.

known measures 274 cm (108 in) in d.b.h. and 37.8 m (124 ft) in height. This tree grows in the Siskiyou National Forest, OR *(1)*.

Yield data are difficult to find. The "average" stand (fig. 3) contains 1,086 trees per hectare (440/acre), 8.9 cm (3.5 in) and larger in d.b.h., and would yield slightly more than 409 m^3/ha (5,845 ft^3 or 65 cords/acre). In 60-year-old mixed-hardwood stands on good sites in the northern Sierra Nevada, black oak produces 76 m^3/ha (1,085 ft^3 or 12.1 cords/acre).

Rooting Habit—Various investigators have described the rooting system of black oak as having no taproot but large spreading roots *(18)*; as deep and long lived; with a strong taproot; and possessing strong laterals, more or less deep, depending on depth to ground water *(3)*.

Observations at road cuts indicate the general rooting pattern of this oak. Usually, from one to several vertical roots extend through the soil and penetrate to rock. Then they become lateral and spread out directly above the rock. At fissures, "sinker" roots penetrate the rock itself. A number of roots are found near the surface, probably to exploit the nutrients there.

Reaction to Competition—The tolerance of black oak to shade varies with age. It most accurately can be classed as intolerant because this condition exists throughout most of its life *(9)*. The oak is moderately tolerant in early life, growing well in full sunlight but persisting in dense shade *(31)*. As a sapling and small pole, black oak is less tolerant and often grows tall and thin until it reaches a position in the canopy where it can receive light. The need for top light increases as the tree ages. In dense stands, black oak often fills a "hole" in the canopy, sometimes leaning 15 to 20 degrees to do so. If overtopped, the oak either dies outright or dies back successively each year. Short epicormic branches keep the tree alive for a time, but with continued overtopping, death is inevitable.

Damaging Agents—Fire is black oak's worst enemy. Crown fires kill trees of all ages and ground fires are often fatal. Only a little radiative heat kills the cambium and only a small amount of flame along the trunk leaves long vertical wounds. Bark thickness on mature trees varies from 2 to 5 cm (1 to 2 in), but even the thickest bark provides little insulation to fire. Scars from burning can become a point of entry for fungi. On larger trees, repeated fires often enlarge old scars, sometimes toppling the tree. Fluctuations in weather also cause injury. Heavy, wet snow breaks branches and stems, particularly at forks, and sudden high temperatures following cool wet weather severely injure leaves *(25)*.

California black oak is especially susceptible to fungi. Heart rot of the bole and large limbs of living trees, caused mainly by two pathogens, *Inonotus dryophilus* and *Laetiporus sulphureus*, is the principal damage *(24)*. These rots enter the tree through broken branches or open wounds resulting from fire or logging. Both fungi often reduce the bole and large limbs of older, decadent trees to mere shells. The hedgehog fungus (*Hydnum erinaceus*) also is found in the heartwood of living trees and *Polyporus adustus* in the sapwood, though neither is prevalent.

By the time a natural black oak stand is 85 years old, the proportion of infected trees begins to increase rapidly. Almost 40 percent of trees 110 to 120 years old show incipient heart rot *(21)*. Rotation age of stands grown for wood products could be influenced by this incidence-age relationship.

Another serious pathogen, *Armillaria mellea*, causes decay of the roots and butt of older decadent black oak. Sometimes it weakens the root system so much that the tree topples over on a perfectly calm, still day *(36)*. This pathogen is indigenous in black oak, but younger vigorous trees do not seem to be affected by it.

A comparatively recent damaging agent to black oak in the San Bernardino Mountains of southern California is air pollution. Although the oak appears less susceptible to air pollution damage than associated conifers, radial growth has decreased in some trees *(12)*. Where high ambient oxidant air pollution levels are chronic, damage to California black oak is expected to be significant *(26)*.

One virulent pathogen that black oak escapes, and indeed is resistant to, is *Heterobasidion annosum* *(14)*. For this reason, California black oak is being planted in numerous infection centers in southern California forests where conifers are dead or dying.

California black oak is prone to several leaf diseases including the oak leaf fungus (*Septoria quercicola*), oak anthracnose (*Gnomonia veneta*), powdery mildews (*Microsphaera* and *Sphaerotheca* spp.), a leaf blister fungus (*Taphrina caerulescens*), a leaf rust (*Cronartium* spp.), and true mistletoe (*Phoradendron villosum* subsp. *villosum*). Damage from each of these pests has not been determined but loss of growth increment probably is minor.

Animal damage to black oak is mostly from browsing. Foliage is eaten during all seasons, but especially in spring when new growth is tender and in winter when twigs are eaten. Deer eat acorns, seedlings, sprouts, and foliage. Even in midsummer, newly germinated seedlings with acorns attached often are consumed *(8)*. Occasionally, browsing is fatal. In Mendocino County, CA, for example, a deer population of 1/2.4 ha (1/6 acres) almost eliminated oak over large areas of the Coast Range. Cattle also browse black oak, but in national forests, at least, their numbers are declining.

Many insects derive sustenance from black oak. The damage is usually secondary, reducing growth but seldom killing trees. Among sucking insects, the pit scales (*Asterolecanium minus* and *A. quercicola*) have the greatest potential for damage *(4)*. The most destructive insect, however, is probably the carpenterworm (*Prionoxystus robiniae*), whose larvae mine the wood of trunk and limbs and cause injuries that appear later as defects in lumber *(16)*.

Other insects are capable of heavy damage, especially when infestations become epidemic. The Pacific oak twig girdler (*Agrilus angelicus*) is the most damaging insect to oak in southern California during drought years *(4)*. In northern California, the California oakworm (*Phryganidia californica*) is noted for defoliating trees. So is the fruit-tree leafroller (*Archips argyrospila*) which, in 1968, caused heavy damage throughout a wide area in the Sacramento River drainage.

Special Uses

Several attributes qualify the wood of California black oak for commercial use: attractive grain and figure for paneling and furniture, hardness and finishing qualities for flooring, and strength properties for pallets, industrial flooring, and other uses *(19)*. The forks of open-grown black oaks were put to good use in the 1870-80's in Mendocino County.

Those of specific dimensions were used as "naturally assembled" ship keels and ribs. Wood products currently produced are high grade lumber and pallets, industrial timbers, sawdust for mulching, and bulk and prepackaged firewood. The wood is prized for fuelwood and in some areas unrestricted cutting is eliminating oak stands.

Although not presently utilized, black oak acorns, high in edible oils, are a potential source for thousands of tons of human food *(38)*.

Genetics

Two natural hybrids are recognized: *Quercus* × *ganderi* C. B. Wolf *(Q. agrifolia* × *Q. kelloggii)* and *Quercus* × *moreha* Kellogg *(Q. kelloggii* × *wislizenii)*. Another hybrid, *Quercus* × *chasei (Q. agrifolia* × *kelloggii)* has been described in Monterey and Santa Clara Counties, CA.

Of the hybrids, *Q. moreha* is by far the most widespread, ranging throughout California and even found, though rarely, in south-central Oregon. The tree is distinguished readily in the winter by its sparse evergreen foliage in contrast to the completely deciduous black oak. New leaves in spring form a dense mass of shiny green foliage on the hybrid.

Forma cibata, a form by which black oak has been described, is a low shrub common to steep, rocky, talus slopes at higher elevations. Although described as a true shrub form, this status is questionable. No criteria are known for distinguishing between it and scrubby black oak trees.

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Quercus laevis Walt. Turkey Oak

Fagaceae Beech family

Richard F. Harlow

Turkey oak (*Quercus laevis*), also called Catesby oak or scrub oak, is a small, moderately fast to fast-growing tree found on dry sandy soils of ridges, pinelands, and dunes, often in pure stands. This oak is not commercially important because of its size, but the hard, close-grained wood is an excellent fuel. The acorns are an important food to wildlife. Turkey oak is so named for its 3-lobed leaves which resemble a turkey's foot.

Habitat

Native Range

Turkey oak (figs. 1, 2) is limited to the dry pinelands and sandy ridges of the southeastern Coastal Plain from southeast Virginia to central Florida and west to southeast Louisiana *(14)*. It reaches its maximum development in a subtropical climate. This

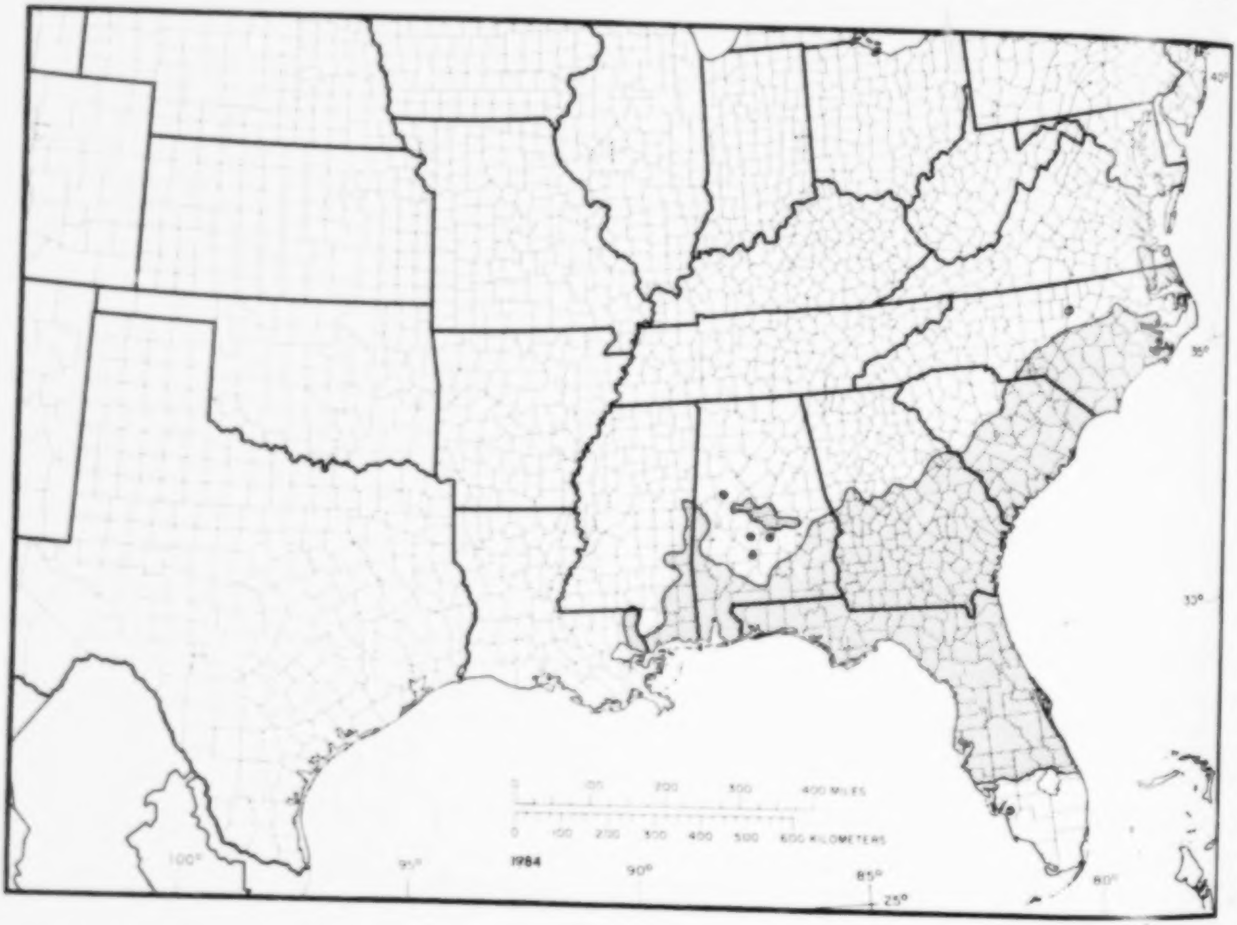

Figure 1—*The native range of turkey oak.*

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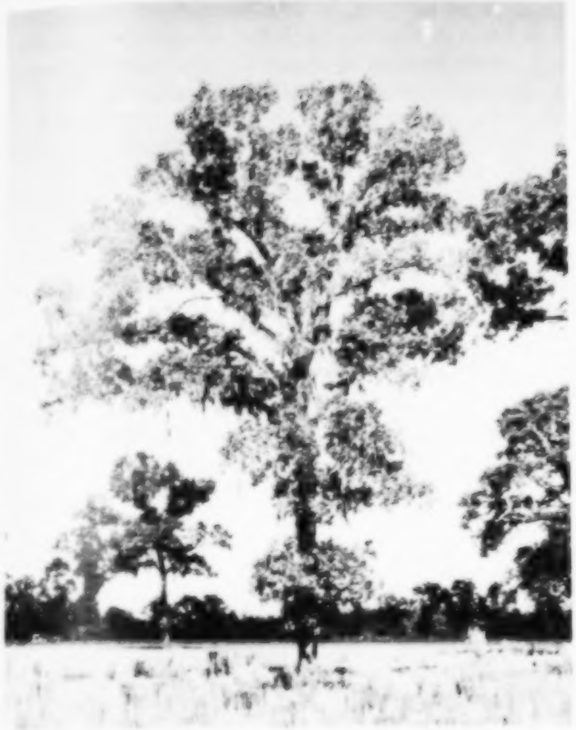

Figure 2—*Turkey oak.*

oak grows on approximately 3.5 to 4 million ha (9 to 10 million acres) of land in Florida alone *(27)*.

Climate

Temperatures average 7° to 16° C (45° to 60° F) during January and 27° to 28° C (80° to 82° F) during July. Rainfall ranges from 1040 to 1780 mm/yr (41 to 70 in), averaging 1350 mm (53 in). Growing season precipitation ranges from 250 to 460 mm (10 to 18 in) during March, April, and May; 300 to 660 mm (12 to 26 in) during June, July, and August; and from 200 to 460 mm (8 to 18 in) during September, October, and November. The mean length of the frost-free period ranges between 270 and 330 days *(18)*.

Soils and Topography

Turkey oak grows on dry pinelands and sandy ridges or high dunes. These hilly regions lie primarily in the central peninsula of Florida and the sandhills of the two Carolinas. Soils of these droughty sites are Entisols; they often lack clay-size particles within 3.0 m (10 ft) of the surface, are low in organic matter, and are strongly acid. Depth to water table is more than 152 cm (60 in) *(18,21)*.

Associated Forest Cover

Turkey oak is commonly associated with longleaf pine *(Pinus palustris)*, bluejack oak *(Quercus incana)*, and sand (dwarf) post oak *(Q. stellata* var. *margaretta)*. Depending on location it can also be associated with sand pine *(Pinus clausa)*, laurel oak *(Quercus laurifolia)*, southern red oak *(Q. falcata)*, live oak *(Q. virginiana)*, blackjack oak *(Q. marilandica)*, sand hickory *(Carya pallida)*, mockernut hickory *(C. tomentosa)*, and black cherry *(Prunus serotina)*. Understory, depending on the part of the range considered, can include sassafras *(Sassafras albidum)*, persimmon *(Diospyros virginiana)*, pawpaw *(Asimina* spp.), dwarf huckleberry, deerberry, and tree sparkleberry *(Vaccinium* spp.), New Jersey tea *(Ceanothus americanus)*, gopher-apple *(Geobalanus oblongifolius)*, blackberry *(Rubus* spp.), crooked wood *(Lyonia* spp.), scrub hickory *(Carya floridana)*, myrtle oak *(Quercus myrtifolia)*, Chapman oak *(Q. chapmanii)*, sand live oak *(Q. virginiana* var. *geminata)*, and poison-sumac *(Toxicodendron vernix)*. Common ground cover plants include wiregrass *(Aristida* spp.), bracken *(Pteridium aquilinum)*, *Heterotheca* spp., and legumes *(10,21,24)*.

Three forest cover types include turkey oak *(6)*—Longleaf Pine–Scrub Oak (Society of American Foresters Type 71), Southern Scrub Oak (Type 72), and Sand Pine (Type 69).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Turkey oak is monoecious; staminate flowers are borne in naked aments and pistillate flowers in flowered spikes on the same tree *(23)*. The flowers appear in April or late spring. The fruit (a nut, called an acorn) requires 2 years to mature *(25)*.

Seed Production and Dissemination—In central Florida, turkey oak seed production was sampled on 40 trees over a 7-year period *(10)*. The trees failed to produce fruit only 1 year. Average fruit production, based on an average weight per fallen acorn of 2.55 g (0.09 oz) and an average stand density of 178 trees per hectare (72/acre), was 150 ± 27 kg/ha (134 ± 24 lb/acre). Production ranged from a high of 312 ± 76 kg/ha (278 ± 68 lb/acre) to a low of 24 ± 8 kg/ha (21 ± 7 lb/acre).

Acorn production for two turkey oak stands and 10 open-grown trees was studied at Georgetown, SC *(8)*.

Average annual acorn production for open-grown trees, 13 cm (5 in) in d.b.h. and larger, was 0.18 to 0.54 kg (0.4 to 1.2 lb) per tree and 0.05 to 0.23 kg (0.1 to 0.5 lb) per tree for those of similar size growing under stand conditions. Average weight of green, fresh acorns varied from 4.6 to 6.0 g (0.16 to 0.21 oz). Variation in acorn crops occurred annually between stands and individual trees.

Stand density has a minimum influence on acorn production of individual trees. A mature, unthinned stand of 370 trees per hectare (150/acre) may be thinned up to 50 percent without significantly reducing acorn production when the best producers are left in the stand *(10)*.

The heavy fruits do not roll far from their source. Small animals do not help their dissemination to any marked degree; instead they prevent dispersion by eating the fruits. Rodents are the worst offenders *(21)*.

Seedling Development—Based on two samples, average germinative capacity was 82 percent after a cold stratification period of 60 to 90 days *(21)*. Seeds were placed in medium sand with a day temperature equal to 27° C (81° F) and a night temperature of 23° C (73° F). For one sample, cleaned seeds per kilogram totaled 871 (395/lb) *(23)*.

In the sandhills, acorns are subjected to great extremes of temperature if they are not buried under litter. If conditions are favorable, germination takes place the following spring. Germination is hypogeal. Studies of dormancy and afterripening indicated that turkey oak acorns required an outdoor afterripening of only 2 months. This may make it possible for them to become established during the very early spring before they are faced with the summer heat and high temperature.

Vegetative Reproduction—Oak root collars sprout freely. Fire kills the aboveground stem but stumps sprout vigorously, resulting in an increased number of stems *(25)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Turkey oak is a moderately fast to fast-growing tree with a relatively short life span. It grows to a height of 6 to 15 m (20 to 50 ft), rarely to 20 m (65 ft) *(5)*. The largest turkey oak on record, growing near Branford, FL, measured 25 m (83 ft) in height, with a d.b.h. of 66 cm (25.8 in), and a crown spread of 20 m (67 ft) *(19)*. In northwest Florida, the density of turkey oak in a stand of large hardwoods, 9 cm (3.5 in) in d.b.h. or larger, ranged from 7,351 to 7,467 stems/ha (2,975 to 3,022 stems/acre), while in another stand of small hardwoods, 9 cm (3.5 in) in d.b.h. or smaller, density ranged from 8,107 to 8,261 stems/ha (3,281 to 3,343/acre). Turkey oak accounted for 75 percent of the hardwood stems in the stand of large hardwoods and 72 percent in the stand of smaller hardwoods *(2)*.

The relative abundance of noncommercial species in 57 study plots located in the sandhills of northwest Florida, based on stems per hectare (acre), was as follows: turkey oak, 4,584 (1,855) or 47 percent of the total; sand post oak, 1,735 (702); bluejack oak, 1,527 (618); saw-palmetto *(Serenoa repens)*, 1,273 (515); and persimmon, 566 (299) *(4)*.

A volume table (table 1) was developed from data on turkey oaks growing on a deep sand ridge in Putnam County, FL *(7)*. Measurements of 20 mature turkey oaks growing on the Ocala National Forest in central Florida, averaging 38.9 years in age and ranging from 24 to 49 years, was as follows *(10)*:

Item	Average	Range
Age, yr	39.9	24 to 49
Height, m	10.3	7.6 to 12.5
D.b.h., cm	18.5	15.7 to 24.6
Radial wood growth for 10 years, cm	2.3	1.4 to 5.1
Ground area covered by crown, m^2	21.55	7.6 to 36.9
Height, ft	33.9	25 to 41
D.b.h., in	7.3	6.2 to 9.7
Radial wood growth for 10 years, in	0.92	0.56 to 2.02
Ground area covered by crown, ft^2	232	82 to 397

Table 1—Merchantable volume for turkey oak (adapted from *7*)[1]

D.b.h.	Total height 5.0 m or 16 ft	10.0 m or 33 ft	15.0 m or 49 ft	20.0 m or 66 ft
cm		*m^3*		
10	—	0.02	0.05	0.09
14	0.02	0.06	0.10	0.13
18	0.08	0.12	0.16	0.19
22	0.16	0.19	0.23	0.26
26	0.25	0.28	0.32	0.35
30	0.35	0.39	0.42	0.46
34	0.47	0.51	0.54	0.58
38	0.60	0.64	0.67	0.71
in		*ft^3*		
3.9	—	0.6	1.8	3.0
5.5	0.9	2.1	3.4	4.6
7.1	3.0	4.2	5.5	6.7
8.7	5.6	6.9	8.1	9.3
10.2	8.8	10.0	11.2	12.5
11.8	12.4	13.7	14.9	16.2
13.4	16.6	17.9	19.1	20.4
15.0	21.3	22.6	23.8	25.0

[1] The table was constructed from the regression: merchantable volume in ft^3 = [illegible] (d.b.h.)^2 ^{5}0.757 (total height) − 3.57. Standard error of the estimate = ±1.00 ft^3. Each volume represents the merchantable portion of the stem from a 0.3 m (1.0 ft) stump to the top of the last 1.2 m (4.1 ft) section with a minimum diameter outside bark of 10.2 cm (4.0 in).

Rooting Habit—Initially, the young turkey oak seedling develops a long taproot. As the seedling grows, the root system develops much more extensively in comparison with the aboveground stem. This well-developed root system provides the plant with a greater absorbing surface for possible contact with minerals and remote supplies of water as the surface sand dries out. Roots from separate trees will graft together *(21,22)*.

Reaction to Competition—The effects of logging are favorable to turkey oak which is classed as intolerant of shade. Fire favors the dominance of more fire-resistant pine. Where fire is an almost yearly occurrence, the herbaceous understory does not become thick enough to support fire of sufficient severity to seriously retard turkey oak. When the understory has accumulated for 3 to 4 years it will carry fire hot enough to kill even large turkey oaks *(13)*.

Establishment of pine plantations on the sandhills of northeast Florida necessitates almost complete removal of oaks and grass that compete for soil moisture on these dry sites *(3,4)*.

The following characteristics of turkey oaks have contributed to their predominance on sandhill sites: short afterripening period of the acorns with subsequent germination before adverse conditions of summer; vertical leaf orientation, a phototropic response, which may act as a protective mechanism against intense light and high temperature; and development of a deep, extensive root system in seedlings *(21)*.

Damaging Agents—Turkey oak was found to be susceptible to oak wilt *(Ceratocystis fagacearum)* in north-central South Carolina *(26)*. In central Florida curculionid weevils *(Curculio* spp.) were found in 81.2 percent of the acorn crop from 40 turkey oak trees in 1960 and in 36.2 percent of the crop from the same trees in 1962 *(10)*.

Special Uses

The seasoned wood of turkey oak is excellent fuel and widely used as a firewood. The bark and twigs contain valuable materials for tanning leather. The light-brown to light reddish-brown wood is close-grained, hard, and heavy, but the trees do not grow large enough, on the average, to have timber value *(5,16,23,24)*.

Turkey oak acorns have been identified as a major food source for black bear, white-tailed deer, northern bobwhite, and wild turkey in Florida *(9,11,17,20)*. Site preparation decreased game-food plants by virtually eliminating the scrub oak and the acorns and browse they produce, and, except for the first few years after chopping, substituted no food plants of comparable value *(12)*. In longleaf pine–turkey oak habitat in central Florida, complete removal of all turkey oaks on 259-ha (1-mi^2) plots caused a pronounced reduction in deer use, especially during the fall *(1)*.

Genetics

Turkey oak hybridizing with southern red, bluejack, laurel, and water *(Q. nigra)* oaks results in the following hybrids *(15)*: *Quercus falcata* (*Q.* × *blufftonensis* Trel.), *Q. incana* (*Q.* × *asheana* Little), *Q. laurifolia* (*Q.* × *mellichamp* Trel.), and *Q. nigra* (*Q.* × *walteriana* Ashe).

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Quercus laurifolia Michx. Laurel Oak

Fagaceae Beech family

Robert D. McReynolds and E. A. Hebb

Laurel oak *(Quercus laurifolia)* is also called Darlington oak, diamond-leaf oak, swamp laurel oak, laurel-leaf oak, water oak, and obtusa oak. There has been a long history of disagreement concerning the identity of this oak *(11)*. It centers on the variation in leaf shapes and differences in growing sites *(5)*, giving some reason to name a separate species, diamond-leaf oak *(Q. obtusa)*. Here they are treated synonymously. Laurel oak is a rapid-growing short-lived tree of the moist woods of the southeastern Coastal Plain. It has no value as lumber but makes good fuelwood. It is planted in the South as an ornamental. Large crops of acorns are important food for wildlife.

Habitat

Native Range

Laurel oak (fig. 1) is native to the Atlantic and Gulf Coastal Plains from southeastern Virginia to southern Florida and westward to southeastern

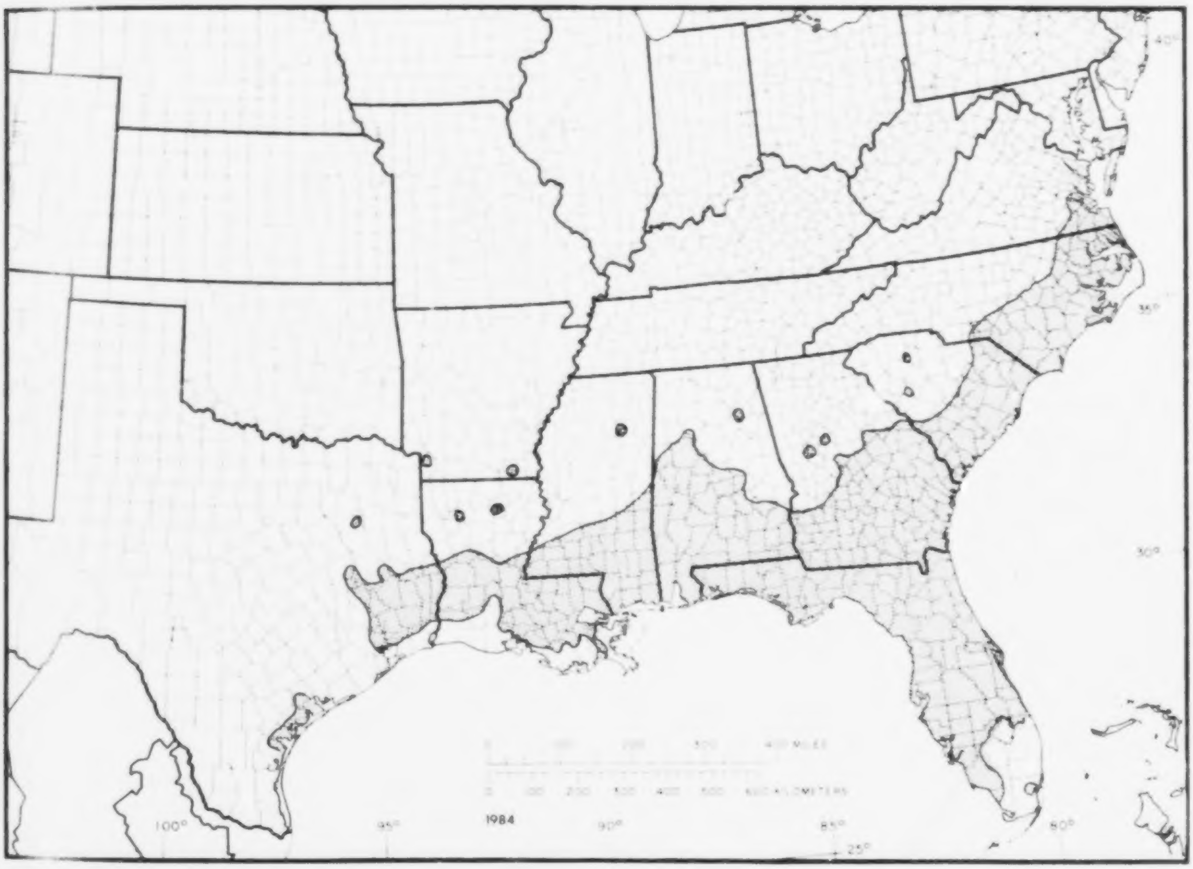

Figure 1—*The native range of laurel oak.*

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Texas with some island populations found north of its contiguous natural range. The best formed and largest number of laurel oaks are found in north Florida and in Georgia.

Climate

Rainfall averages between 1250 and 1500 mm (49 to 59 in) a year over the natural range of laurel oak. From 500 to 1000 mm (20 to 39 in) of this is received during the growing season from April to September, except during occasional years when there is a summer or fall drought lasting 1 to 3 months. Average annual temperatures across the range of laurel oak vary from 16° to 21° C (61° to 70° F). Extreme lows range from -1° to -18° C (30° to 0° F). Extreme highs range from 38° to 43° C (100° to 109° F). Relative humidities seldom fall below 60 percent. The frost-free season extends from 220 days in the north to more than 320 days in south Florida.

Soils and Topography

Laurel oak is most common on alluvial flood plains. It tolerates the wetter sites in association with other oak species but does not withstand continuous or prolonged flooding. It is most often found growing in sandy soil near rivers and along the edges of swamps if not too frequently flooded. Laurel oak grows in the hammocks of central Florida and on sand hills adjacent to swamps in west Florida. It is also planted as an ornamental with little regard to soil type *(14)*. Laurel oak grows best on Ultisols and Inceptisols.

Associated Forest Cover

Laurel oak is a major species in the forest cover type Willow Oak–Water Oak–Diamond-leaf (Laurel) Oak (Society of American Foresters Type 88) *(5)*. Diamond-leaf oak makes up most of the stand in this type where drainage is poor, sometimes forming almost pure stands, while laurel oak grows on the better drained sites such as sandy banks of streams.

Laurel oak is also an associated species in the following forest cover types: Cabbage Palmetto (Type 74), Loblolly Pine (Type 81), Longleaf Pine–Slash Pine (Type 83), Sweetgum–Willow Oak (Type 92), and Baldcypress–Tupelo (Type 102).

Associated tree species may include Nuttall oak *(Quercus nuttallii)*, red maple *(Acer rubrum)*, green ash *(Fraxinus pennsylvanica)*, sweetgum *(Liquidambar styraciflua)*, swamp hickory *(Carya glabra)*, honeylocust *(Gleditsia triacanthos)*; and on wetter sites water hickory *(Carya aquatica)*, waterlocust *(Gleditsia aquatica)*, and overcup oak *(Q. lyrata)*. On better drained sites laurel oak may be associated with spruce pine *(Pinus glabra)*, loblolly pine *(P. taeda)*, swamp chestnut oak *(Q. michauxii)*, and cherrybark oak *(Q. falcata* var. *pagodifolia) (5)*.

In Florida, southern magnolia *(Magnolia grandiflora)*, American beech *(Fagus grandifolia)*, pignut hickory *(C. glabra* var. *glabra)*, Carolina basswood *(Tilia caroliniana)*, and scrub hickory *(C. floridana)* are associates.

Around Charleston, SC, laurel oak's tree associates include redbud *(Cercis canadensis)*, American beech, yellow-poplar *(Liriodendron tulipifera)*, southern magnolia, spruce pine, white oak *(Q. alba)*, and Carolina basswood. Associated shrubs and vines include crossvine *(Bignonia capreolata)*, sweet rhododendron *(Rhododendron canescens)*, sweetleaf *(Symplocos tinctoria)*, and muscadine grape *(Vitis rotundifolia)*.

Associated shrubs and small trees include American hornbeam *(Carpinus caroliniana)*, Virginia-willow *(Itea virginica)*, poison-sumac *(Toxicodendron vernix)*, swamp cyrilla *(Cyrilla racemiflora)*, littleleaf cyrilla *(C. racemiflora* var. *parvifolia)*, sebastian bush *(Sebastiana ligustrina)*, dahoon *(Ilex cassine)*, possumhaw *(I. decidua)*, swamp dogwood *(Cornus stricta)*, sweet pepperbush *(Clethra alnifolia)*, tree lyonia *(Lyonia ferruginea)*, buttonbush *(Cephalanthus occidentalis)*, pinckneya *(Pinckneya pubens)*, and rhododendron *(Rhododendron* spp.). Associated vines include coral greenbrier *(Smilax walteri)*, laurelleaf greenbrier *(S. laurifolia)*, and Alabama supplejack *(Berchemia scandens) (14)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Laurel oak is monoecious; stamens and pistils are in separate flowers on the same tree. Staminate flowers are borne in naked catkins developing from leaf axils of the previous year. Pistillate flowers are usually solitary, on short, stout, glabrous stalks developing from axils of leaves of the current year. Flowering occurs in February and March, about the time the last of the previous year's leaves are shed *(15)*. Pollen is wind disseminated. Flower crops are abundant almost every year.

Seed Production and Dissemination—Laurel oak acorns are brown to almost black, 13 mm (0.5 in) in both diameter and length, with one-quarter or less enclosed in a thin saucerlike cup *(7)*. Acorn production begins when the trees are 15 to 20 years old;

they soon become prolific bearers. Acorns require 2 years to mature and fall to the ground during late September and October. Some of the acorn caps remain attached to the tree. There are about 1,235 sound, uncapped laurel oak acorns per kilogram (560/lb). Acorn dissemination is mainly by squirrels but is aided by gravity and runoff during rains. Most sound acorns sink but some float and are carried a long distance *(14,15)*.

Seedling Development—Acorns of trees in the black oak group, to which laurel oak belongs, show embryo dormancy and germinate the following spring after fall ripening. Germination is hypogeal *(15)*. Laurel oak acorns exhibit only mild dormancy. Without any cold stratification, germinative capacity in two samples of laurel oak acorns was 50 percent *(15)*. In another test, germination of laurel oak acorns, with one exception, was unaffected or only slightly increased by 30 days' soaking in distilled water *(10)*. There are few or no published descriptions of laurel oak seedling development after acorn germination.

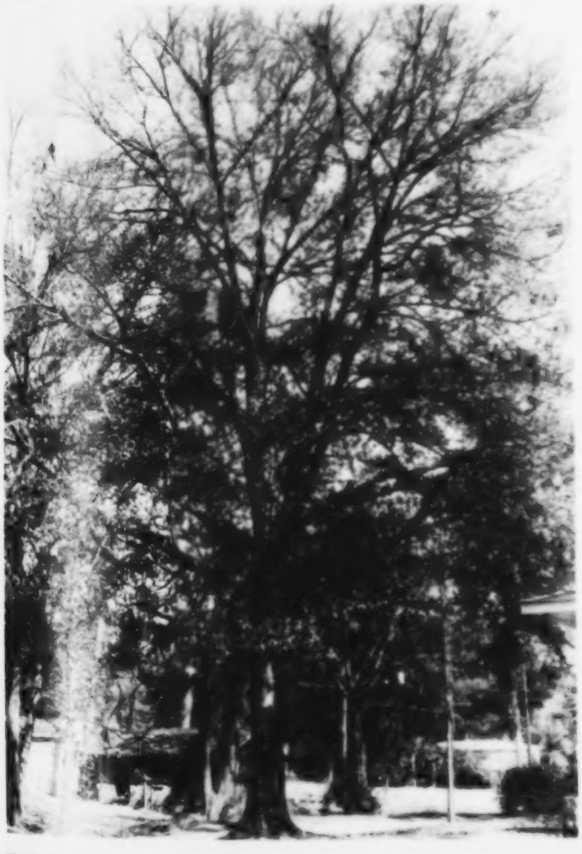

Figure 2—A laurel oak, 69 cm (27 in) in d.b.h., open grown as a shade tree in Florida.

Vegetative Reproduction—When cut or burned, a young laurel oak produces many sprouts from the base of its stump. Older trees do not sprout vigorously, and their sprouts are more susceptible to decay than those of young trees *(14)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Laurel oak (fig. 2) grows rapidly and usually matures in about 50 years which has led to its wide use as an ornamental *(14)*.

Southeastern Forest Survey data show the largest volume of laurel oak in the 25- to 36-cm (10- to 14-in) d.b.h. classes with average total heights from 18 to 21 m (59 to 69 ft). It has the poorest timber quality of the red and black oaks, producing sawtimber only on the best sites. It is marketed mainly as pulpwood. Considering live volume of trees 13 cm (5 in) in d.b.h. and up from a stump height of 30 cm (12 in) and a top diameter of 10 cm (4 in), laurel oak has an average annual mortality of 1.1 percent, an average annual growth of 4.1 percent, and an average annual removal of 2.0 percent. It shares a high mortality rate with water oak because of their relatively thin bark among oaks and susceptibility to fire. Only about half of laurel oak's growth is harvested each year. In an assessment of aboveground biomass of trees 2.5 cm (1 in) in d.b.h. and larger, laurel oak constituted 3.4 percent of associated hardwood biomass and 8.4 percent of the oak biomass. A conservative estimate of growth is 6.4 cm (2.5 in) in d.b.h. every 10 years *(9)*.

Rooting Habit—Laurel oak develops a large well-defined taproot on upland sands as observed on trees uprooted for road construction *(12)*. No published information on the rooting habits of laurel oak was found.

Reaction to Competition—Laurel oak is classed as shade tolerant from seedling to mature tree and often becomes established and grows up through the dense canopy of a swamp border. Natural pruning is poor and large limbs persist on the bole many years, even under a dense canopy *(14)*.

Damaging Agents—Fire is especially hazardous to laurel oaks. They are frequently killed by even light ground fires and heartrots are common in trees subject to occasional burns *(14)*.

Laurel oak is host to the general oak-feeding insects but no serious insect problem is mentioned in the literature. Several species of *Curculio* weevils infest acorns, including those of laurel oak *(1)*.

Although not seriously harmed themselves, laurel oak, water oak, and willow oak are the three most susceptible hosts for the alternate stage of fusiform rust *(Cronartium quercuum* f. sp. *fusiforme)* of southern pines. Laurel oak is also susceptible to oak leaf blister *(Taphrina caerulescens)*, actinopelte spot *(Actinopelte dryina)*, and canker rots by various fungi *(8)*.

Special Uses

Laurel oak has been widely planted in the South as an ornamental, perhaps because of the attractive leaves from which it takes its common name.

Large crops of laurel oak acorns are produced regularly and are an important food for white-tailed deer, raccoons, squirrels, wild turkeys, ducks, quail, and smaller birds and rodents *(4)*. Comparing volumes of the 10 most heavily used fall and winter food items found in 423 rumen samples of deer from Florida, laurel oak acorns rated fifth, sixth, or seventh highest in quantity consumed in a 6-year period *(6)*. Acorns were most frequently consumed and in the largest quantity by 32 wild turkeys whose crops were examined in Florida; of the identified acorns, laurel oak was second only to live oak in quantity and frequency *(13)*.

Genetics

In the past, laurel oak and diamond-leaf oak have been considered by some to be two varieties or even separate species *(11)*. Trees first recognized as laurel oak were on well-drained sandy banks of streams whereas diamond-leaf oak was found on poorly drained flat sites *(5)*.

Burke concluded that laurel oak itself is of hybrid origin, intermediate between and derived from willow oak and water oak *(2,3)*. His work is based on a leaf-shape index applied to seedlings grown from acorns collected on the North Carolina Outer Banks and at Chapel Hill, NC. He states that laurel oak is not found outside the ranges of the two supposed parental species. This would appear true based on most published maps showing the range of willow oak available in 1961 and 1963, when Burke's publications appeared. However, the range map for willow oak published in 1965 *(14)* shows willow oak to be absent in the southeastern half of Georgia and peninsular Florida where laurel oak grows in abundance, leaving some doubt that laurel oak is the hybrid between willow and water oak *(14)*.

The following hybrids with *Quercus laurifolia* as one parent have been recognized *(11)*: *Quercus falcata* (*Q.* × *beaumontiana* Sarg.), *Q. incana* (*Q.* × *atlantica* Ashe), *Q. laevis* (*Q.* × *mellichampii* Trel.), and *Q. marilandica* (*Q.* × *diversiloba* Tharp ex A. Camus).

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Quercus lyrata Walt. Overcup Oak

Fagaceae Beech family

J. D. Solomon

Overcup oak *(Quercus lyrata)*, also called swamp post oak, swamp white oak, and water white oak, is quite tolerant of flooding and grows slowly on poorly drained flood plains and swamp lands of the Southeastern United States. It may take 30 years before overcup oak produces acorns. Wildlife use them as food. The quality of the lumber varies greatly and the wood may check and warp during seasoning. It is cut and sold as white oak.

Habitat

Native Range

Overcup oak (fig. 1) inhabits the wetter sites in bottom lands of the Coastal Plain from Delaware and Maryland south to Georgia and northwestern Florida; west to eastern Texas. It grows northward in the Mississippi Valley to southeastern Oklahoma,

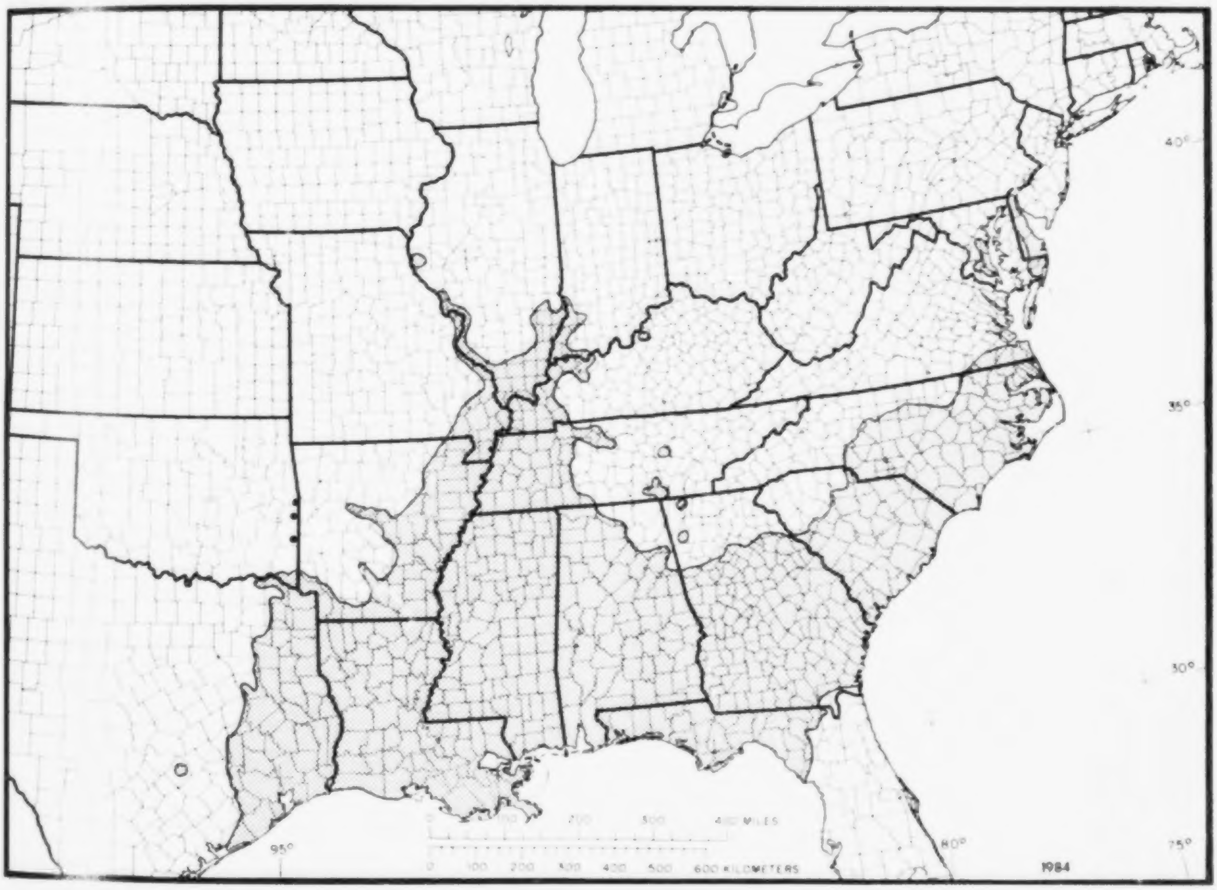

Figure 1.—*The native range of overcup oak.*

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southeastern Missouri, southern Illinois, southwestern Indiana, and western Kentucky *(8)*.

Climate

The climate is warm and humid throughout the range of overcup oak *(10)*. In the region where the species grows best, total precipitation averages 1140 to 1520 mm (45 to 60 in) per year of which 510 to 760 mm (20 to 30 in) is received during the April-to-September growing season. Snow fall is 2.5 to 12.5 cm (1 to 5 in). The mean January temperature is about 7° C (45° F) and mean July temperature is about 28° C (82° F). Temperature extremes are -29° C (-20° F) and 46° C (115° F).

Soils and Topography

Overcup oak (fig. 2) is found on poorly drained, alluvial, clayey soils mainly on southern river flood plains *(13)*. It is most prevalent on low lying clay or silty clay flats in first bottoms and terraces of the larger streams *(15)*. It is also quite common on the edges of swamps, sloughs, and bayous; in poorly drained depressions or sink holes on ridges; and in shallow swamps and sloughs *(12)*. Overall it is most commonly found growing on soils in the orders Inceptisols and Alfisols. The overcup oak–water hickory type is often predominant on poorly drained backwater flats and small shallow sloughs commonly flooded for a few weeks after the growing season begins *(10)*. Overcup oak is one of the trees most tolerant of flooding *(3)*. Since it leafs out a month or more later than most species, it is better able to endure submergence from late spring floods. In tests, overcup oak survived continuous flooding for at least two growing seasons. In spite of its natural occurrence on wet clay sites, overcup oak grows best on sites with better drainage and soil texture *(10)*.

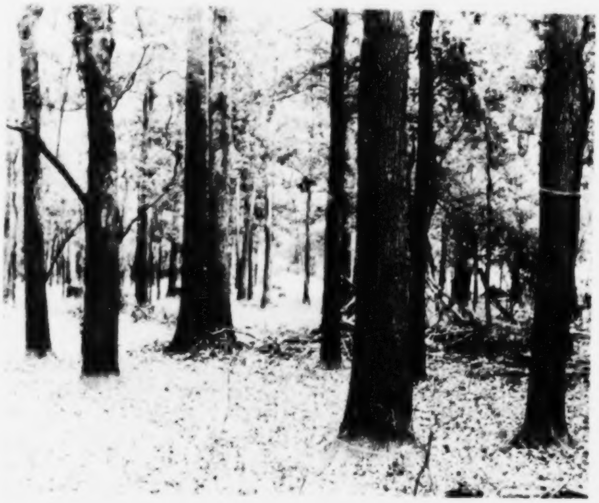

Figure 2—*Bottom land stand of overcup oak.*

Associated Forest Cover

Overcup oak is usually a dominant species only in the forest cover type Overcup Oak–Water Hickory (Society of American Foresters Type 96) *(4)*. The species most commonly associated with overcup oak are water hickory *(Carya aquatica)*, willow oak *(Quercus phellos)*, Nuttall oak *(Q. nuttallii)*, American elm *(Ulmus americana)*, cedar elm *(U. crassifolia)*, green ash *(Fraxinus pennsylvanica)*, sugarberry *(Celtis laevigata)*, waterlocust *(Gleditsia aquatica)*, common persimmon *(Diospyros virginiana)*, and red maple *(Acer rubrum)*.

Overcup oak is a minor component in the following forest cover types: Sweetgum–Willow Oak (Type 92), Sugarberry–American Elm–Green Ash (Type 93), Baldcypress (Type 101), and Baldcypress–Tupelo (Type 102).

Trees infrequently associated with overcup oak include sweetgum *(Liquidambar styraciflua)*, honeylocust *(Gleditsia triacanthos)*, cottonwood *(Populus deltoides)*, black willow *(Salix nigra)*, water oak *(Quercus nigra)*, and sycamore *(Platanus occidentalis)*. Common shrub or small tree associates include swamp-privet *(Forestiera acuminata)*, hawthorn *(Crataegus* spp.), roughleaf dogwood *(Cornus drummondii)*, buttonbush *(Cephalanthus occidentalis)*, and planertree *(Planera aquatica)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Male and female flowers appear while the leaves are developing during April and May in the Mississippi Delta. The staminate flowers are borne in naked aments (catkins) with the pistillate flowers in flowered spikes on this monoecious tree *(11)*. The fruit, an acorn, is 12 to 25 mm (0.5 to 1 in) long, has a flattened spherical shape, usually broader at the base than long, and may be entirely covered by a scaly cup—hence the common name of the species, overcup oak. The acorns mature in 1 year, ripen by September or October, and fall soon after.

Seed Production and Dissemination—Trees begin bearing seeds about 25 years of age and good seed crops are produced every 3 to 4 years. Late freezes, after the flower buds have started to open, have been known to kill the flowers and thus destroy the seed crop. Cleaned seeds average 308/kg (140/lb) *(11)*. The seeds are disseminated to some extent by flood waters. Animals, especially squirrels, spread some acorns, but overcup acorns are less preferred than those of many other oak species. Acorn insects, particularly acorn weevils (Curculio spp.), may destroy a major part of the seed crop during light seed years, but are less important during good seed years.

Seedling Development—In flooded areas the acorns remain dormant over winter and germinate in the spring after the surface waters recede, making overcup acorns one of the few of the white oak group that do not germinate until spring *(10)*. Germination is hypogeal *(11)*. Natural reproduction is prolific, but many young seedlings are killed by inundation during the first few growing seasons. Seeds germinate readily either in the open or in the shade, but because of the tree's relative intolerance to shade, reproduction persists only in openings *(13)*. Seedlings and stump sprouts generally are able to grow through all competing ground cover except heavy peppervine, which sometimes develops into a tangled mat *(10)*. Successful regeneration depends on complete absence of fire and adequate seed.

Growth of seedlings is rated as average but varies greatly with site, soil, and the kind and degree of competition *(13)*. Eight-year-old trees on a backwater flat were found to vary from 12 to 75 mm (0.5 to 3 in) in diameter at groundline *(10)*. There is little information on early height growth, but based on site index figures, height growth might be expected to average 45 to 60 cm (18 to 24 in) per year *(2)*.

Vegetative Reproduction—Stumps of small trees sprout vigorously but not consistently; therefore, stump sprouts cannot be relied upon as a silvicultural practice to regenerate the stand. Successful whip, cleft, and bark grafts of overcup oak and its hybrids have been reported, but T-bud grafts have failed and cuttings from hybrids do not root *(10)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Overcup oak (fig. 3) produces a medium-size tree 18 to 27 m (60 to 90 ft) in height and 61 to 76 cm (24 to 30 in) in diameter *(10,12)*. Maximum height rarely exceeds 30 m (100 ft) and diameters exceeding 91 cm (36 in) are uncommon. Maximum age attained is about 400 years *(6)*. Overcup oak commonly develops a short trunk, frequently crooked or spiraled, and a broad, wide-spreading, open crown or major branches bearing relatively few smaller branches *(12)*. The bole is rarely clear for any great length; however, on the better sites it may develop a trunk clear of large branches having lengths of 12 m (40 ft) or more. Height growth of overcup oak is slower than many of its associates, causing it to be overtopped easily, which may partially account for the short crooked boles. Diameter growth for trees free to grow in unmanaged stands on average bottomland sites averages about 5.0 to 6.4 cm (2 to 2.5 in) in 10 years *(13)*. On the best sites it may grow 10 cm (4 in) in 10 years, but old trees on low flats subject to backwater overflow may grow only 5 cm (2 in) in diameter in 50 years. Under management on average or better sites, the overcup oak–water hickory type should yield about 2.8 m³/ha (200 fbm/acre) (International quarter-inch log rule) or more per year *(1)*.

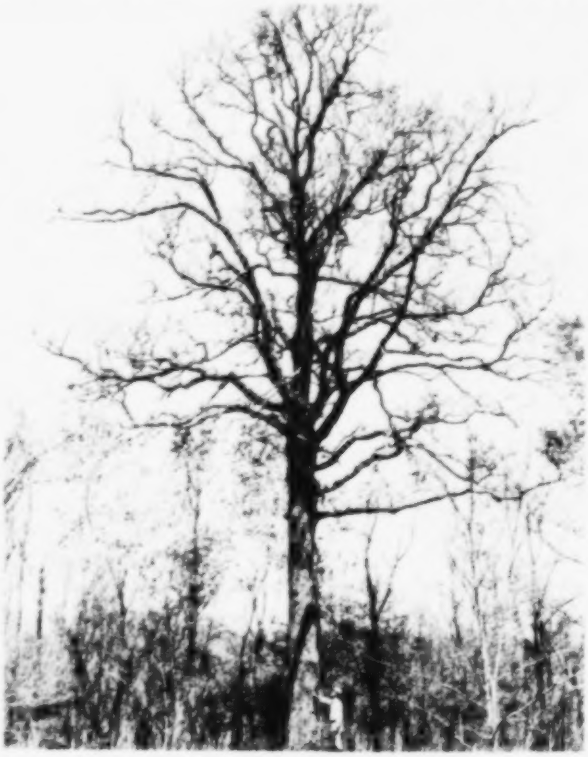

Figure 3—*Single large tree of overcup oak.*

The quality of overcup oak varies greatly throughout its range but is generally medium to poor due to insects, shake, and other factors. Overcup oak is said to produce only about half as much No. 1 Common and Better lumber as the other white oaks *(5)*. Next to post oak it has been referred to as the "poorest of the white oaks" (13). In fact, it has been stated that "overcup oak from overflow sites in the Mississippi Delta is one of the most obstinate, cantankerous woods that ever a kiln operator tried to dry" (7). For many years operators discriminated against overcup oak on overflow sites because it could not be dried without serious checking and honeycombing. This no-cut practice reached a point where overcup oak dominated many cutover sites. Quality is generally poorest in the southern half of the Mississippi River Delta. North of the latitude from Eudora, AR, to Greenwood, MS, it is of fair to very good quality. Within these areas, quality tends to be best on the better drained second bottoms and terrace soils and toward the outer edges of the Delta, and especially on the older geologic formations to the north (15). In the bottoms of the larger streams in Georgia and the Carolinas its quality is usually good.

Rooting Habit—Overcup oak develops a shallow, saucer-shaped root system. The heavy clay soils and wet sites where overcup oak typically grows restrict root development to relatively shallow depths. Although the seedlings initially produce taproots, these are replaced by a lateral root system. The root system of one large tree consisted of many small branching roots with no large main roots.

Reaction to Competition—Overcup oak is classed as intermediate in its response to competition and shade (10,13). Seeds germinate profusely beneath complete canopy, but the seedlings invariably succumb or at least die back to the root collar within 3 years unless released. Many stands of overcup oak owe their development to tolerance of early season flooding that kills off earlier flushing species. It is frequently a lack of competition rather than an affinity for the backwater sites that allows this species to dominate.

Because of its tolerance of flooding, overcup oak growing on low backwater flats is classified as a climax species (10). But on better sites where it grows in combination with other oaks, green ash, and sweetgum, it becomes a subclimax tree. Because of its slow growth rate, poor quality, drying difficulties, and low commercial value, woodsmen usually try to favor other species of better quality.

Damaging Agents—Overcup oak is notorious for many defects, a reputation due largely to wood borers and the rapid decay of heartwood following fire injuries (6). Loss from insect borer degrade in lumber sawn from sample overcup oak logs in Arkansas, Louisiana, and Mississippi, updated to 1980 lumber prices, amounted to \$22.80/m^3 (\$130/ thousand fbm) (9). The carpenterworm (*Prionoxystus robiniae*) and red oak borer (*Enaphalodes rufulus*) are the two most damaging large trunk borers of sawtimber—producing galleries in the wood 12 to 18 mm (0.5 to 0.7 in) in diameter and 15 to 25 cm (6 to 10 in) long (14). The white oak borer (*Goes tigrinus*) is damaging to young trees but limits its attacks to saplings and poles up to about 20 cm (8 in) in diameter.

This oak, growing on sites subjected to backwater flooding from December through June, is sometimes rendered almost worthless by a spot-worm borer (*Agrilus acutipennis*), which leaves a tiny frass-packed hole surrounded by a dark stained area, descriptively named grease spot. This defect seriously degrades lumber and ruins its wood for tight cooperage.

Another common defect in overcup oak lumber is bark pocket, caused by several borers but particularly the red oak borer and carpenterworm, which initiate attacks in the bark and cambium area but succumb before galleries are made in the sapwood. When these spots heal, pockets of ingrown bark and stained wood are formed. These remain in the trunk as the tree grows and appear as defects in lumber and other products.

Other insects, including the defoliators, usually are not very harmful, but periodic outbreaks such as the 1952 outbreak of the basswood leafminer, *Baliosus ruber*, can severely weaken trees and reduce growth.

Except for the heart rots (*Poria* spp., *Polyporus* spp., *Hericium* spp.), which follow injuries, especially those due to fire, diseases are not serious in overcup oak. A viruslike disorder of overcup oak seedlings has been studied but appears to be either physiologically induced or of genetic origin.

Special Uses

The utility of overcup oak varies extremely with site, fire damage, and degree of insect and decay defect (13). Logs harvested from the best overcup oak sites may be used for lumber and sometimes tight cooperage, but the wood is frequently worthless for factory lumber and other quality products. Moreover, checking during seasoning often prevents general use even as ties and timbers. The species is sometimes used for ornamental purposes. The trees provide habitat and the acorns supply mast for wildlife.

Genetics

Population Differences

Wide differences in quality of overcup oak occur over its range—generally the better quality is found in its northern and eastern range. These differences, however, are probably due to response to site and seasonal flooding patterns rather than to genetic differences. Limited studies of juvenile variation within a small geographic area have not provided any evidence of genetic variation among localities.

Hybrids

Quercus lyrata hybridizes with *Q. alba; Q. durandii; Q. bicolor* (*Q. × humidicola* Palmer); *Q. macrocarpa* (*Q. × megaleia* Laughlin); Q. *michauxii* (*Q. × tottenii* Melvin); *Q. stellata* (*Q. × sterrettii* Trel.); and *Q. virginiana* (*Q. × comptoniae* Sarg.) *(8)*. A cross between *Q. lyrata* and *Q. virginiana* is reported to be promising for propagation and dissemination *(10)*. This hybrid is a semievergreen and has a higher growth rate than either parent. However, its vegetative propagation has presented problems.

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Quercus macrocarpa Michx. Bur Oak

Fagaceae Beech family

Paul S. Johnson

Bur oak (*Quercus macrocarpa*), also known as blue oak, mossycup oak, mossy-overcup oak, and scrub oak, has the largest acorns of all native oaks and is very drought resistant. It grows slowly on dry uplands and sandy plains but is also found on fertile limestone soils and moist bottomlands in mixture with other hardwoods. In the west, it is a pioneer tree invading prairie grasslands, and it is planted frequently in shelterbelts. The acorns become an important source of food to wildlife. The wood is commercially valuable and marketed as white oak. The comparative ease with which bur oak can be grown makes it a fine tree for streets or lawns.

Habitat

Native Range

Bur oak (figs. 1, 2) is widely distributed throughout the Eastern United States and the Great Plains. It ranges from southern New Brunswick, central Maine, Vermont, and southern Quebec, west through Ontario to southern Manitoba, and extreme southeastern Saskatchewan, south to North Dakota, extreme southeastern Montana, northeastern Wyoming, South Dakota, central Nebraska, western Oklahoma, and southeastern Texas, then northeast to Arkansas, central Tennessee, West Virginia, Maryland, Pennsylvania, and Connecticut. It also grows in Louisiana and Alabama.

Climate

Bur oak is one of the most drought resistant of the North American oaks. In the northwestern part of its range, the average annual precipitation is as low as 380 mm (15 in). Here, the average minimum temperature is 4° C (40° F), and the average growing season lasts only 100 days. To the south bur oak grows in areas having an average precipitation exceeding 1270 mm (50 in) per year, minimum temperatures of -7° C (20° F), and a growing season of 260 days. The best development of the bur oak occurs in southern Illinois and Indiana, where the average annual precipitation is about 1140 mm (45 in), minimum temperature is -29° C (-20° F), and the growing season is 190 days *(5)*.

Soils and Topography

Bur oak on uplands is often associated with calcareous soils. In the "driftless" area of southwestern Wisconsin, it is commonly found on limestone ridges; in Kentucky, it is more prevalent on limestone soils than on soils derived from shales and sandstone *(5)*. In western Iowa, it can be found as a dominant on soils of either limestone or sandstone origin. Throughout much of the prairie region of the Midwest, bur oak is found on droughty sandy plains, black prairie loams, and on loamy slopes of south and west exposure. Toward the western edge of its range, such as in eastern Kansas, it is more abundant on the more moist north-facing slopes than on south-facing slopes *(2)*. Bur oak often dominates severe sites with thin soils, heavy claypan soils, gravelly ridges, and coarse-textured loessial hills. The predominant soil orders on which bur oak is found include Alfisols in the central and southern parts of its range, and Mollisols and Spodosols in the western and northern parts of its range, respectively.

Bur oak is also an important bottom-land species throughout much of its range. In the Central States Region and southward, it is found on moist flats and on hummocky bottoms. Northward, in southern Michigan, it has been found in high densities on slightly elevated ridges within wet bottom-land forests occupying old glacial lake beds and drainage ways *(20)*.

Bur oak frequently forms a fringe between the prairie and upland forest in northern Illinois and eastern Iowa, notably at the outer edges of "breaks" and bluffs along streams and around limestone outcrops. It is a valuable timber species on favorable bottom-land sites within this region.

Within the Great Plains Region, it is frequently found in stream bottoms and stream terraces. In North Dakota, bur oak is a major component of the flood-plain forests of the Missouri River *(11)*. Here it may predominate in old stands on high terraces near the edge of the flood plain. It is absent in low terraces near the center of the flood plain. Along adjacent draws and upper slopes, it becomes the first tree established along prairie edges. Bluffs along the Missouri River and its tributaries in eastern Nebraska are frequently covered with bur oaks that range in size from small trees near the base of bluffs to shrublike growth near the top.

In the Black Hills of western South Dakota and the Bear Lodge Mountains of northeastern Wyoming,

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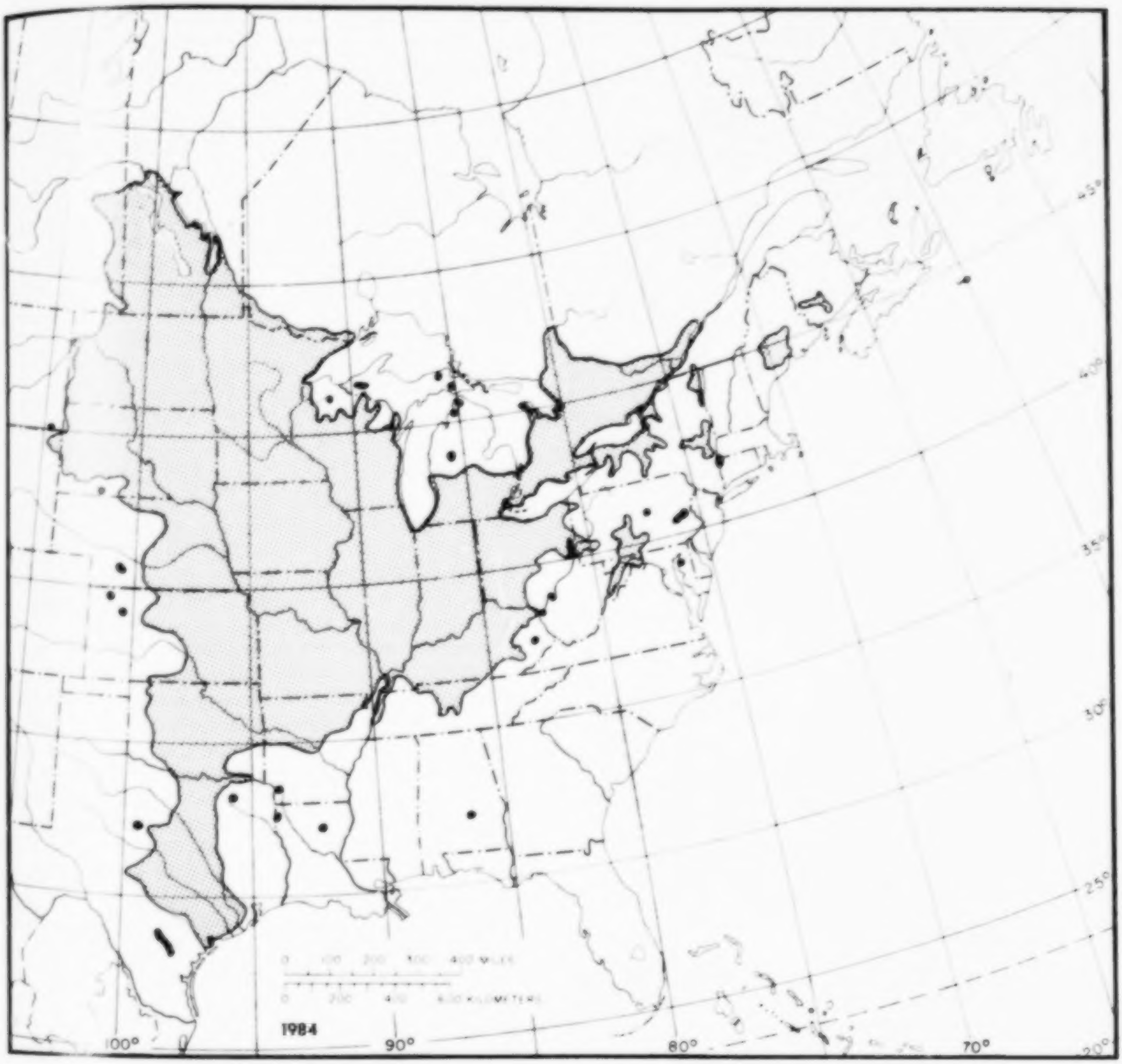
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Figure 1—*The native range of bur oak.*

bur oak grows at low elevations between the ponderosa pine forest and the grasslands *(21)*. Here, it ranges in size from a shrub under a pine canopy at higher elevations to a tree up to 21 m (69 ft) tall along stream bottoms at lower elevations.

Associated Forest Cover

Because of its tolerance to a wide range of soil and moisture conditions, bur oak is an associate of many other trees. In pure or nearly pure stands, it forms

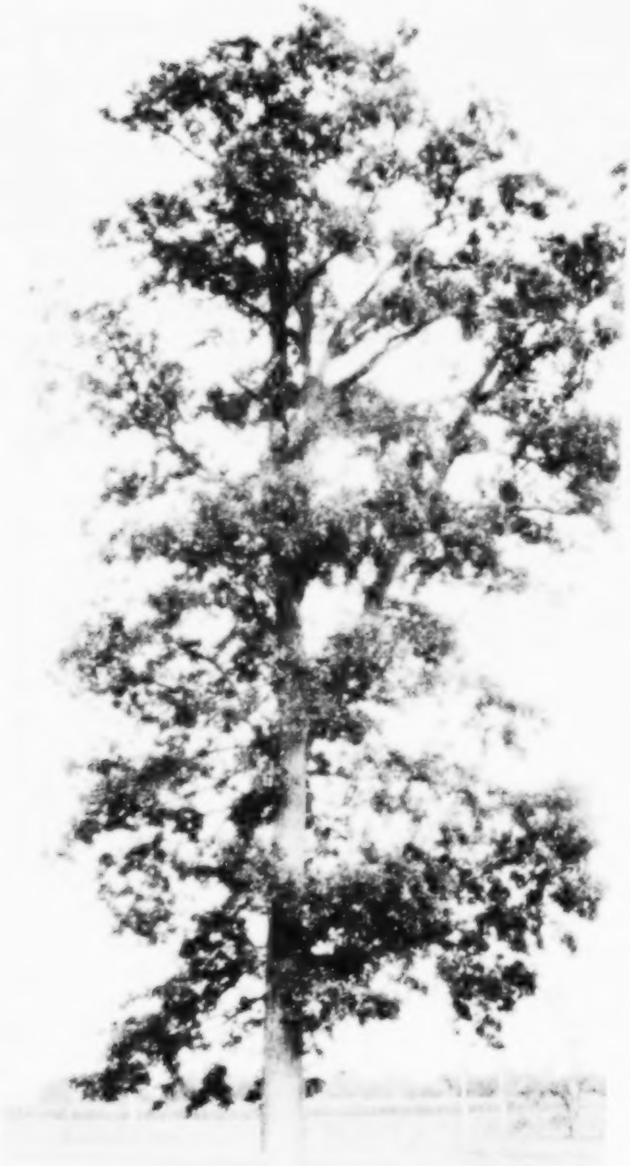

Figure 2—*Bur oak.*

the forest cover type Bur Oak (Society of American Foresters Type 42, eastern forests; Type 236, western forests) *(6)*. It is also an important associate in six other types: Northern Pin Oak (Type 14), Aspen (Type 16), Black Ash–American Elm–Red Maple (Type 39), White Oak (Type 53), Pin Oak–Sweetgum (Type 65), and Hawthorn (Type 109).

In southern bottom-land cover types such as Pin Oak–Sweetgum, important associates of bur oak are pin oak (*Quercus palustris*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), American elm (*Ulmus americana*), blackgum (*Nyssa sylvatica*), swamp white oak (*Quercus bicolor*), willow oak (*Q. phellos*), overcup oak (*Q. lyrata*), green ash (*Fraxinus pennsylvanica*), Nuttall oak (*Quercus nuttallii*), swamp chestnut oak (*Q. michauxii*), white oak (*Q. alba*), shellbark hickory (*Carya laciniosa*), and shagbark hickory (*C. ovata*). Associated shrubs and vines on these sites include possumhaw (*Ilex decidua*), poison-ivy (*Toxicodendron radicans*), and trumpet-creeper (*Campsis radicans*).

In more northerly bottom-land types, such as Black Ash–American Elm–Red Maple, important associates of bur oak include black ash (*Fraxinus nigra*), American elm, red maple, American basswood (*Tilia americana*), silver maple (*Acer saccharinum*), swamp white oak, sycamore (*Platanus occidentalis*), and eastern cottonwood (*Populus deltoides*). Common shrub associates include speckled alder (*Alnus rugosa*), vacciniums (*Vaccinium* spp.), red-osier dogwood (*Cornus stolonifera*), and poison-sumac (*Toxicodendron vernix*).

Important associates of bur oak in the cover type White Oak include northern red oak (*Quercus rubra*), black oak (*Q. velutina*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and post oak (*Q. stellata*), mockernut hickory (*Carya tomentosa*), pignut hickory (*C. glabra*), and bitternut hickory (*C. cordiformis*). In this type, associated shrubs and vines include vacciniums, sumacs (*Rhus* spp.), witch-hazel (*Hamamelis virginiana*), wild grape (*Vitis* spp.), Virginia creeper (*Parthenocissus quinquefolia*), and poison-ivy.

On the drier sites in the northwestern part of its range, bur oak grows in mixed stands of American elm, green ash, bitternut hickory, and white oak, and sometimes as nearly pure oak stands. In North Dakota, for example, the cover type Bur Oak accounts for about 19 percent of the forest land. Bur oak is also the major tree of oak savannas ("oak openings") of the prairie–forest transition zone in Wisconsin, Minnesota, Iowa, and Illinois *(3,5,8,12)*.

Shrubs are especially abundant in the bur oak forest of the plains region. Predominant among them are American hazelnut (*Corylus americana*), coralberry (*Symphoricarpos orbiculatus*), and smooth sumac (*Rhus glabra*); common associates on the prairie borders are hawthorn (*Crataegus* spp.), wolfberry (*Symphoricarpos occidentalis*), and prairie crabapple (*Malus ioensis*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Bur oak is monoecious; male and female flowers in separate catkins are borne on the current year's branchlets. It flowers shortly after the leaves appear, from about the first of April in the southern part of its range to about mid-June in the north *(5)*. Pollen from one tree appears to germinate better on the stigmas of another, favoring cross pollination.

Seed Production and Dissemination—The acorns ripen within the year and drop from the tree as early as August or as late as November. Germination usually occurs soon after seedfall, but acorns of some northern trees may remain dormant through winter and germinate the following spring *(5)*.

Bur oaks bear seed up to an age of 400 years, older than reported for any other American oak. The minimum seed-bearing age is about 35 years, and the optimum is 75 to 150 years *(5,16)*. Good seed crops occur every 2 to 3 years, with no crops or light crops in intervening years. The acorns are disseminated by gravity, by squirrels, and to a limited extent by water.

Seedling Development—Various conditions influence seedling development *(5)*. In Iowa uplands, germination of acorns and early development of bur oak were best where litter had been removed. Germination is hypogeal *(16)*. When covered by litter, acorns were most susceptible to pilferage by rodents, and the newly developed seedlings were more liable to fungus and insect attack. In a Nebraska study, about 30 percent of acorns germinated within 1 month after seedfall, and the new seedlings were less susceptible to freezing than those of white oak. Under controlled environment, bur oak seedlings grew fastest at a daytime temperature of 31° C (88° F) and a nighttime temperature of 19° C (66° F) *(23)*. The relatively high daytime temperature and a high (70 percent) relative humidity were necessary to obtain more than one flush of shoot growth during the first growing season. When grown under continuous light, bur oak also produced a greater number of shoot flushes than under normal light *(19)*.

As a bottom-land species, bur oak is relatively intolerant of flooding, and a mesic, fertile environment is required for seedling establishment *(11,14)*. In open bottom lands, reproduction of bur oak may be prolific, but first-year mortality may be 40 to 50 percent when seedling submersion is 2 weeks or longer during the growing season. For shorter periods of growing-season submersion, seedling mortality is only about 10 to 20 percent. Although bur oak seedlings can endure flooding for up to 30 consecutive days during the growing season, root growth is greatly reduced, thus reducing drought tolerance after flood waters have receded *(22)*.

Bur oak seedlings have also been found to be efficient users of water, based on studies of the ratio of transpiration resistance to CO_2 uptake resistance *(25)*. In this characteristic, it was slightly exceeded by black oak but was more efficient than northern red oak, white oak, and sugar maple for leaf temperatures up to 35° C (95° F). The large number and area of stomata per unit leaf area in bur oak are associated with potentially high transpiration rates *(4)*.

Root growth of juvenile bur oaks is rapid, and the taproot penetrates deeply into the soil before the leaves unfold. At the end of the first growing season, bur oak roots have been found at depths of 1.37 m (4.5 ft), with a total lateral spread of 76 cm (30 in). This strong early root development, along with high water-use efficiency, may explain why bur oak can pioneer on droughty sites and can successfully establish itself in competition with prairie shrubs and grasses *(5)*.

Vegetative Reproduction—Vigorous sprout growth follows the burning or cutting of pole-size or smaller bur oaks; but except for seedling sprouts, the quality and form of sprout stems are poor. Some sprout growth is also produced by larger trees, but the effect of size and age of parent tree on sprouting vigor and quality has not been determined *(5)*. Five years after prescribed burning in Minnesota, 60 percent of bur oaks 10 to 41 cm (4 to 16 in) d.b.h. had produced sprouts. Sprouts occurred in clumps averaging 21 live stems and the three tallest live stems per clump averaged 2.5 m (8.2 ft) tall *(18)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Bur oak is a slow-growing tree *(5)*. In 12- to 16-year-old plantations on Iowa upland sites, average annual height growth ranged from 0.09 to 0.52 m (0.3 to 1.7 ft) and diameter growth from less than 2.5 to 6.4 mm (0.1 to 0.25 in). In the shelterbelts of the northern Great Plains, an annual height growth of about 0.3 m (1 ft) was reported for trees kept under clean cultivation.

In Iowa, 10-year d.b.h. growth of bur oak averaged 3.0 cm (1.2 in) for 10- to 20-cm (4- to 8-in) trees, 3.6 cm (1.4 in) for 25- to 36-cm (10- to 14-in) trees, 4.6 cm (1.8 in) for 41- to 51-cm (16- to 20-in) trees, and 5.6 cm (2.2 in) for trees 56 cm (22 in) and larger.

More rapid growth has been reported in Kansas where trees 35 to 40 years old averaged 2.5 cm (1 in) growth in d.b.h. in 3.8 years. Approximately the same growth rate has been observed in the northern Mississippi Delta region.

Bur oak is said to have reached a height of 52 m (170 ft) and a d.b.h. of 213 cm (84 in) in the lower Ohio Valley. On the better sites, mature trees generally grow 24 to 30 m (80 to 100 ft) tall, 91 to 122 cm (36 to 48 in) in d.b.h., and live 200 to 300 years. Characteristically, they have a massive, clear trunk and a broad, open crown of stout branches.

In the oak openings of southern Wisconsin and in the prairie border areas to the south and west, bur oak often is found in nearly pure stands *(3,5)*. The trees are widely spaced, short-boled, and often uniform in size. Trees in a 50- to 65-year-old stand in eastern Nebraska were 9 to 12 m (30 to 40 ft) tall and spaced at intervals of 3 to 12 m (10 to 40 ft). Bur oak grows 21 m (70 ft) tall on the fertile soils in this region, but on dry, limestone ridges, the trees may be less than 7.6 m (25 ft) tall at 150 years of age. In Minnesota, bur oak is short lived on the poorer sites.

Timber volumes in the bur oak type of Iowa were estimated to be 15.4 m^3/ha (1,100 fbm/acre), three-fourths of which were bur oak.

Rooting Habit—In the sapling stage, taproot development continues to be rapid, with abundant lateral growth as well. The taproots of 8-year-old saplings in upland clay soils of Missouri were more than 4.3 m (14 ft) long, and primary laterals extended up to 3.4 m (11 ft) *(5)*. In prairie areas, roots of bur oak and hackberry have been found at depths of 3 to 6 m (10 to 20 ft); and a 43-year-old bur oak tree had a lateral spread of 12.5 m (41 ft) although the tree was only 6 m (20 ft) tall. A study of a tree 36 cm (14 in) in d.b.h. revealed that the weight of the roots equaled that of the tops, and root volume was only about 10 percent less than top volume.

Reaction to Competition—Bur oak is classed as intermediate in tolerance to shade *(5)*. Some consider it more tolerant than northern red and white oaks; but on the prairie margins, bur oak stands are often invaded by black oak, white oak, and bitternut hickory. Bur oak reproduction in old white pine–bur oak stands in Minnesota reaches only sapling size before dying from suppression, and these stands are being replaced by maple–basswood communities.

In the wet bottom lands of northern Ohio, bur oak is a secondary species in the cover type Black Ash–American Elm–Red Maple, together with shellbark hickory, green ash, white ash *(Fraxinus americana)*, pin oak, and swamp white oak. On the better drained bottom lands, bur oak may be successfully replaced by more tolerant species such as sugar maple *(Acer saccharum)*, American basswood, and American beech *(Fagus grandifolia)*.

On the prairie edges, bur oak is a pioneer tree, commonly succeeded by northern pin oak *(Quercus ellipsoidalis)*, black oak, white oak, and bitternut hickory. The climax trees on these sites are sugar maple and basswood or sugar maple and beech. Bur oak may be a climax tree with hickory on extremely dry southern aspects and on thin, stony soils. In general, it is a species well adapted to sites ranging from droughty to moderately wet. But, on any given site, it is largely restricted to plant communities in early successional stages *(17)*.

Damaging Agents—Bur oak is attacked by several insects including the following defoliators: redhumped oakworm *(Symmerista canicosta)* in the Northeast, *S. albifrons* in the South, oak webworm *(Archips fervidana)*, oak skeletonizer *(Bucculatrix recognita)*, a leaf miner *(Profenusa lucifex)*, variable oakleaf caterpillar *(Heterocampa manteo)*, June beetles *(Phyllophaga* spp.), and oak lacebug *(Corythucha arcuata) (1,5)*. The latter species may heavily defoliate bur oaks in shelterbelt plantings, especially during dry weather. Attacks from bur oak kermes *(Kermes pubescens)* may distort leaves and kill twigs of bur oak.

Oak wilt *(Ceratocystis fagacearum)* is a less serious problem in bur oak than in members of the red oak group *(5,10)*. Although spread of the disease from infected bur oak to adjacent oaks is infrequent, the disease sometimes spreads through root grafts, and entire groves have been killed by the gradual expansion of the disease from one center of infection.

Bur oak is susceptible to attack by the cotton root rot *(Phymatotrichum omnivorum)* and Strumella canker *(Strumella coryneoidea)*. Half of the trees in a 20-year-old plantation in Pennsylvania became infected with the latter disease; and nearly a fourth of these died. Other fungi that have been isolated from diseased parts of bur oak include Dothiorella canker and dieback *(Dothiorella quercina)*, Phoma canker *(Phoma aposphaerioides)*, Coniothyrium dieback *(Coniothyrium truncisedum)*, and shoestring root rot *(Armillaria mellea)*.

Large bur oak trees are resistant to injury by fire and this, together with resistance to drought and disease, probably account for maintenance of the bur oak "openings" over much of southern Wisconsin at the time of homesteading. The presence of large bur oaks in the sugar maple-basswood community of the Big Woods of Minnesota has been attributed to the tree's thick fire-resistant bark, which enabled it to survive repeated burning and freed it from competition by less fire-resistant species *(5)*.

In the northwest part of its range, bur oak is considered a drought-resistant tree. During severe drought conditions in Iowa, unpastured bur oak stands on dry, exposed slopes were not injured; however, in pastured woods, drought injury occurred, even on protected sites. This was attributed to reduced aeration (caused by trampling) that had limited the growth and efficiency of absorbing roots.

Bur oak is not resistant to flooding, and in two areas where it was permanently flooded it died within 3 years. The species tolerates urban pollution better than most oaks.

Special Uses

Acorns of bur oak make up much of the food of red squirrels and are also eaten by wood ducks, white-tailed deer, New England cottontails, mice, thirteen-lined ground squirrels, and other rodents *(5)*.

On coal-mine spoils with a pH of 5.6 in eastern Kansas, planted bur oak was one of the better performers of several tree species tested *(7)*. After 22 years, it attained a mean height of 8.5 m (28 ft) and a d.b.h. of 12.2 cm (4.8 in). The species is also widely planted in shelterbelts because of its drought tolerance.

Genetics

Population Differences

A northern form of bur oak, *Quercus macrocarpa* var. *olivaeformis*, has been recognized *(5)*. Acorns of this form often germinate in the spring following seedfall rather than soon after falling, and germination is improved by stratification. Acorn size is about half that of the southern form, and the cup is much thinner and smaller. Cleaned seeds average 595/kg (270/lb) compared to only 165/kg (75/lb) for the typical species *(16)*. Where the two forms are found in the same locality, as in eastern Nebraska, the typical bur oak is more common on the moister sites *(5,13)*. Varietal crosses occur in such areas. Photoperiodic ecotypes of bur oak have also been recognized. In one study, shoot growth of a more northerly seed source was about two-thirds of that of a more southerly seed source under short days; under long days, shoot growth of both sources was nearly equal *(24)*.

Hybrids

Bur oak has been known to hybridize with nine species as follows: white oak, *Q.* × *bebbiana* Schneid.; swamp white oak, *Q.* × *schuettei* Trel.; Gambel oak (*Q. gambelii*); overcup oak, *Q.* × *megaleia* Laughlin; swamp chestnut oak, *Q.* × *byarsii* Sudw.; chinkapin oak (*Q. muehlenbergii*), *Q.* × *deamii* Trel.; English oak (*Q. robur*); post oak, *Q.* × *guadalupensis* Sarg.; and live oak (*Q. virginiana*). The cross with white oak, *Q.* × *bebbiana*, Bebb oak, is one of the most frequent of the white oak hybrids and is widespread within the overlapping ranges of the two species *(9)*. The hybrid formed with Gambel oak, a western species, is somewhat unusual in that the two species do not now have overlapping ranges *(15)*.

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Quercus michauxii Nutt. Swamp Chestnut Oak

Fagaceae Beech family

M. B. Edwards

Swamp chestnut oak (*Quercus michauxii*) is known also as basket oak, for the baskets made from its wood, and cow oak because cows eat the acorns. One of the important timber trees of the South, it grows on moist and wet loamy soils of bottom lands, along streams and borders of swamps in mixed hardwoods. The high quality wood is used in all kinds of construction and for implements. The acorns are sweet and serve as food to wildlife.

Habitat

Native Range

Swamp chestnut oak (figs. 1, 2) extends along the Atlantic Coastal Plain from New Jersey and extreme eastern Pennsylvania, south to north Florida, and west to east Texas; it is found north in the Mississippi River Valley to extreme southeast Oklahoma,

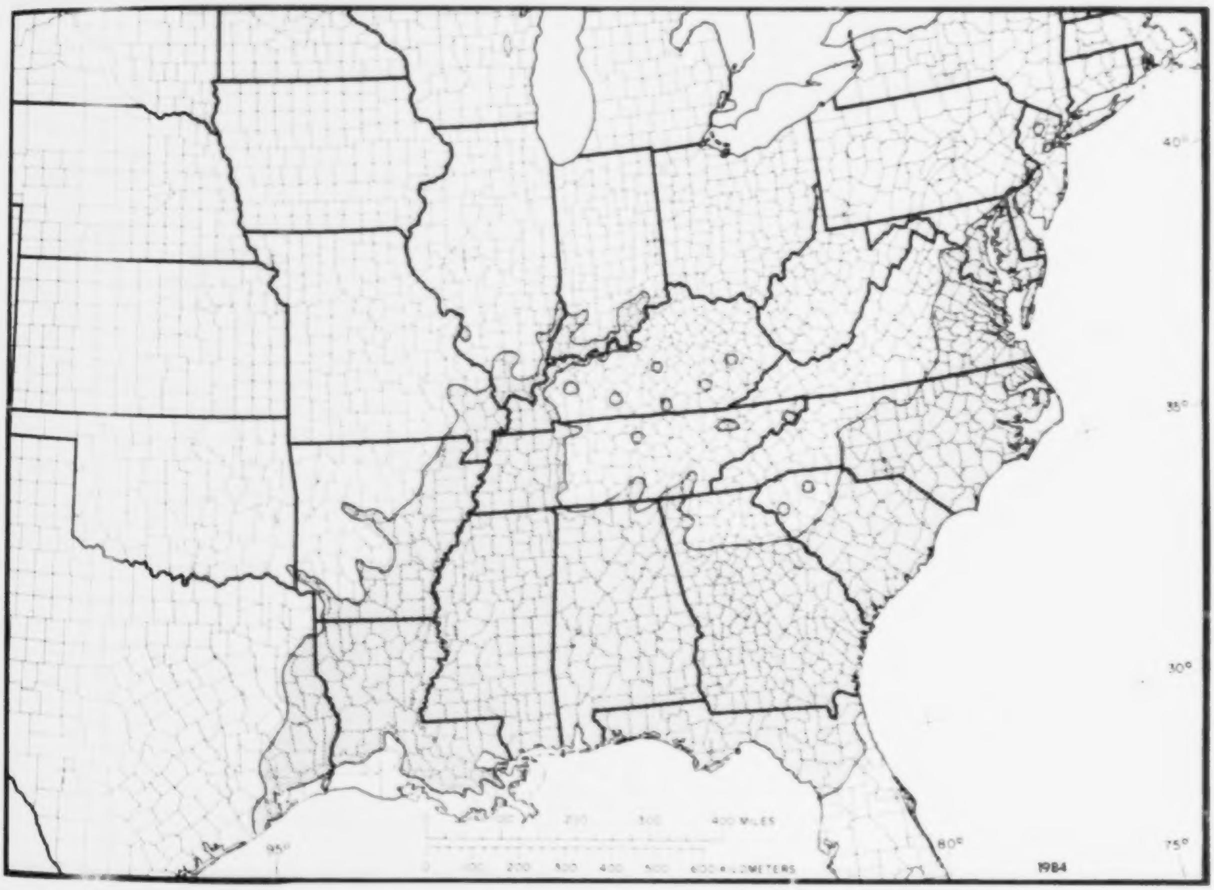

Figure 1—*The native range of swamp chestnut oak.*

The author is Research Ecologist, Southeastern Forest Experiment Station, Asheville, NC.

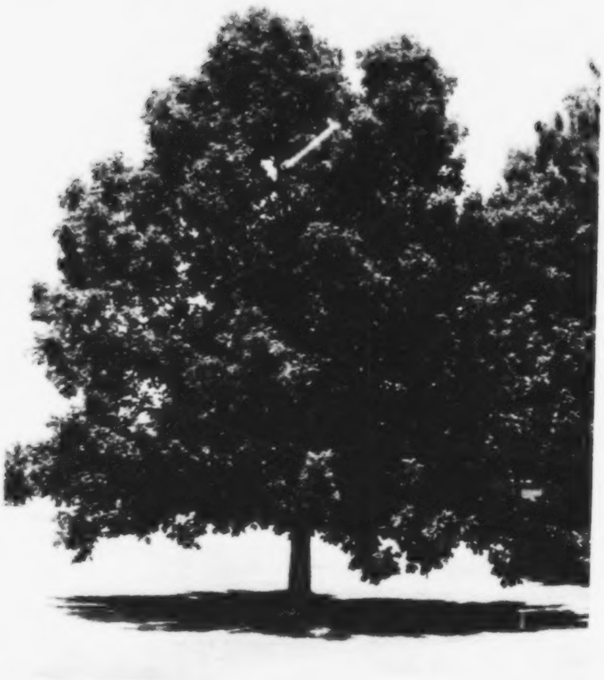

Figure 2—*Swamp chestnut oak.*

Arkansas, southeastern Missouri, southern Illinois, southern Indiana, and locally to southeast Kentucky and eastern Tennessee *(6)*.

Climate

Swamp chestnut oak grows in a humid, temperate climate characterized by hot summers, mild and short winters, and no distinct dry season. The growing season usually averages from 200 to 250 days through the main section of its commercial range. Average annual temperature ranges from 16° to 21° C (60° to 70° F) with an average annual precipitation of 1270 to 1520 mm (50 to 60 in). The average annual maximum temperature is 38° C (100° F) and the average annual minimum is about -9° C (15° F). Approximately 50 percent of the rainfall occurs from April to September. The average noonday relative humidity is about 60 percent in mid-July.

Soils and Topography

The species is distributed widely on the best well-drained loamy first-bottom ridges but is principally found on well-drained silty clay and loamy terraces and colluvial sites in the bottom lands of large and small streams. Bayboro clay loam is representative of the edaphic condition that promotes the best growth of swamp chestnut oak in coastal South Carolina *(4)*. These soils are found in the orders Alfisols and Inceptisols.

Associated Forest Cover

Swamp chestnut oak is found in the forest cover type Swamp Chestnut Oak–Cherrybark Oak (Society of American Foresters Type 91), which varies widely in composition *(2)*. Often swamp chestnut oak and cherrybark oak *(Quercus falcata* var. *pagodifolia)* make up a majority of the stocking although if many species are in the mixture, they may account for only a plurality. Other hardwoods are white ash *(Fraxinus americana)*, shagbark *(Carya ovata)*, shellbark *(C. laciniosa)*, mockernut *(C. tomentosa)*, and bitternut *(C. cordiformis)* hickory. Chief associates are white oak *(Quercus alba)*, Delta post oak *(Q. stellata* var. *paludosa)*, Shumard oak *(Q. shumardii)*, and blackgum *(Nyssa sylvatica)*. Occasionally, sweetgum *(Liquidambar styraciflua)* is important on first-bottom ridges. Minor associates include willow oak *(Quercus phellos)*, southern red oak *(Q. falcata* var. *falcata)*, post oak *(Q. stellata)*, American elm *(Ulmus americana)*, winged elm *(U. alata)*, southern magnolia *(Magnolia grandiflora)*, yellow-poplar *(Liriodendron tulipifera)*, American beech *(Fagus grandifolia)*, loblolly pine *(Pinus taeda)*, and spruce pine *(P. glabra)*.

Among the noncommercial trees or plant associates are devils-walkingstick *(Aralia spinosa)*, painted buckeye *(Aesculus sylvatica)*, pawpaw *(Asimina triloba)*, American hornbeam *(Carpinus caroliniana)*, swamp dogwood *(Cornus stricta)*, dwarf palmetto *(Sabal minor)*, Coastal Plain willow *(Salix caroliniana)*, American snowbell *(Styrax americanus)*, southern arrowwood *(Viburnum dentatum)*, and possumhaw viburnum *(V. nudum)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowers of swamp chestnut oak appear about the same time as the leaves, from April to May. Swamp chestnut oak is monoecious. The fruit or acorn is nearly sessile and may be solitary or paired. Its cup is broad based and covers about one-third of the acorn. Scales on the cup are free to the base and are pubescent. Its dimensions are 1.9 to 3.2 cm (0.75 to 1.25 in) wide by 2.5

to 3.8 cm (1 to 1.5 in) long. The acorns ripen and fall during September and October.

Seed Production and Dissemination—Trees begin to produce seed at about age 20 to 25 and attain their optimum production around age 40. Good seed crops can be expected every 3 to 5 years with poor to fair production the balance of the time. There are about 187 cleaned seeds per kilogram (85/lb), with a range of 77 to 430 (35 to 195) *(7)*. The acorn is very palatable and is eaten by white-tailed deer, wild hogs, and squirrels. Squirrels are perhaps the most helpful animals in disseminating the acorns because they hoard far more than they can actually eat.

Seedling Development—Animal activity greatly inhibits regeneration of swamp chestnut oak from seed. Germination, which is hypogeal, usually starts soon after seedfall, with little or no period of dormancy. A moist, well-drained loam, covered with a light litter layer, provides an excellent seedbed. First-year height growth is related to soil type and drainage. Second-year growth is only related to soil type. This suggests that the species is site sensitive *(4)*.

The stem of the 1-year-old seedling is generally smooth but is covered near the terminal bud with hairs. At first it is reddish brown but becomes gray after the first year, especially at the base. Small, round, inconspicuous lenticels are found on the upper stem. The terminal bud is about 6 mm (0.25 in) long and light brown. The lateral buds are of the same color but are only about 3 mm (0.125 in) long. A cluster of lateral buds around the terminal bud is common.

Vegetative Reproduction—Swamp chestnut oak sprouts, though not prolifically, from roots and stumps.

Sapling and Pole Stages to Maturity

Growth and Yield—Swamp chestnut oak is a medium-size tree and may attain a height of 30.5 m (100 ft) at maturity on better sites. Heights of 18 to 24 m (60 to 80 ft) with trunk diameters of 61 to 91 cm (24 to 36 in) are normal for average sites. The trunk is often free of branches for 15 to 18 m (50 to 60 ft). Stout branches ascend at sharp angles to form a very strong crown. Volume of growing stock on commercial forest land in north Georgia for all diameter classes was 5.97 million m^3 (211 million ft^3). It has also been reported that where swamp chestnut grows with other hardwoods, a total volume in excess of 112 m^3/ha (8,000 fbm/acre) is classed as a heavy sawtimber stand. A heavy pole stand is considered to have more than 432 stems/ha (175 stems/acre) ranging from 13 to 28 cm (5 to 21 in) in diameter at breast height.

Rooting Habit—No information is currently available.

Reaction to Competition—Swamp chestnut oak is classed as intolerant of shade and requires openings for establishment. It normally receives heavy competition from vines, annuals, and brush that are common to most bottom-land hardwood sites. It is reported that when mature, however, this species retards the growth of understory vegetation, probably due to an allelopathic effect *(5)*.

Damaging Agents—Numerous fungi and insects damage swamp chestnut oak. The fungi include wood-decaying species of *Fomes*, *Polyporus*, and *Stereum*. Oak leaf blister (*Taphrina caerulescens*) is sporadic in occurrence, as is oak anthracnose (*Gnomonia veneta*) *(3)*.

Swamp chestnut oak acorns are attacked by weevils such as *Curculio pardalis*, *Conotrachelus naso*, and *C. posticatus*, which consume the seed. Insect defoliators that attack the swamp chestnut are June beetles (*Phyllophaga* spp.), orangestriped oakworm (*Anisota senatoria*), fall cankerworm (*Alsophila pometaria*), spring cankerworm (*Paleacrita vernata*), forest tent caterpillar (*Malacosoma disstria*), yellownecked caterpillar (*Datana ministra*), variable oakleaf caterpillar (*Heterocampa manteo*), and the redhumped oakworm (*Symmerista canicosta*).

Borers that attack healthy trees are the red oak borer (*Enaphalodes rufulus*) in cambium and outer sapwood; carpenterworms (*Prionoxystus* spp.), in heartwood and sapwood; and the Columbian timber beetle (*Corthylus columbianus*), in the sapwood. Those attacking weakened trees include the twolined chestnut borer (*Agrilus bilineatus*), in cambium; and the tilehorned prionus (*Prionus imbricornis*), in roots. Dying trees are attacked by the oak timberworm (*Arrhenodes minutus*) *(1)*.

The golden oak scale (*Asterolecanium variolosum*) kills reproduction and tops in older trees. The gouty oak gall (*Callirhytis quercuspunctata*) and horned oak gall (*C. cornigera*) injure small limbs, while the basswood leafminer (*Baliosus ruber*) attacks the leaves.

Special Uses

Wood from swamp chestnut oak is commercially useful for lumber in all kinds of construction, for agricultural implements, cooperage, fenceposts, baskets, and fuel.

Acorns from swamp chestnut oak serve as mast for various species of birds and mammals.

Genetics

Swamp chestnut oak hybridizes with *Quercus alba* (*Q.* × *beadlei* Trel. ex Palmer); *Q. lyrata* (*Q.* × *tottenii* Melvin); and *Q. macrocarpa* (*Q.* × *byarsii* Sudw.) *(6)*.

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Quercus muehlenbergii Engelm. Chinkapin Oak

Fagaceae **Beech family**

Ivan L. Sander

Chinkapin oak *(Quercus muehlenbergii)*, sometimes called yellow chestnut oak, rock oak, or yellow oak, grows in alkaline soils on limestone outcrops and well-drained slopes of the uplands, usually with other hardwoods. It seldom grows in size or abundance to be commercially important, but the heavy wood makes excellent fuel. The acorns are sweet and are eaten by several kinds of animals and birds.

Habitat

Native Range

Chinkapin oak (fig. 1) is found in western Vermont and New York, west to southern Ontario, southern Michigan, southern Wisconsin, extreme southeastern Minnesota, and Iowa; south to southeastern Nebraska, eastern Kansas, western Oklahoma, and central Texas; east to northwest Florida; and north mostly in the mountains to Pennsylvania and southwestern Massachusetts. There are local populations in the mountains of southeastern New Mexico, Trans-Pecos Texas, and northeastern Mexico *(5)*.

Climate

The climate in which chinkapin oak grows is humid except for the southwestern fringe of its natural range, which is moist subhumid to dry subhumid. The average length of frost-free periods ranges from 120 days in Vermont to 240 days in Texas. Precipitation in the growing season (April 1 to September 30) ranges from an average of about 250 mm (10 in) in southwest Texas to about 2030 mm (80 in) in the southern Appalachians. In southern Indiana and southern Ohio where chinkapin oak grows best, growing season precipitation is from 510 to 640 mm (20 to 25 in) *(4)*.

Soils and Topography

Chinkapin oak is usually found on warm, moist Udalf Alfisols, Dystrochrept Inceptisols, Udoll Mollisols, and Udult Ultisols over much of its range. In the extreme southwestern part of the range chinkapin oak also grows on warm, dry Ustoll Mollisols and Astalf Alfisols *(9)*. Chinkapin oak is generally found on well-drained upland soils derived from limestone or where limestone outcrops occur. Occasionally it is found on well-drained limestone soils along streams. It appears that soil pH is strongly related to the prescence of chinkapin oak, which is generally found on soils that are weakly acid (pH about 6.5) to alkaline (above pH 7.0). It grows on both northerly and southerly aspects but is more common on the warmer southerly aspects. It is absent or rare at high elevations in the Appalachians *(3,4)*.

Associated Forest Cover

Chinkapin oak is rarely a predominant tree, but it grows in association with many other species. It is a component of the forest cover type White Oak-Black Oak-Northern Red Oak (Society of American Foresters Type 52) and the Post Oak-Blackjack Oak (Type 40) *(2)*.

It grows in association with white oak *(Quercus alba)*, black oak *(Q. velutina)*, northern red oak *(Q. rubra)*, scarlet oak *(Q. coccinea)*, sugar maple *(Acer saccharum)*, red maple *(A. rubrum)*, hickories *(Carya* spp.), black cherry *(Prunus serotina)*, cucumbertree *(Magnolia acuminata)*, white ash *(Fraxinus americana)*, American basswood *(Tilia americana)*, black walnut *(Juglans nigra)*, butternut *(J. cinerea)*, and yellow-poplar *(Liriodendron tulipifera)*. American beech *(Fagus grandifolia)*, shortleaf pine *(Pinus echinata)*, pitch pine *(P. rigida)*, Virginia pine *(P. virginiana)*, Ozark chinkapin *(Castanea ozarkensis)*, eastern redcedar *(Juniperus virginiana)*, bluejack oak *(Quercus incana)*, southern red oak *(Q. falcata)*, blackgum *(Nyssa sylvatica)*, and winged elm *(Ulmus alata)* also grow in association with chinkapin oak. In the Missouri Ozarks a redcedar-chinkapin oak association has been described.

The most common small tree and shrub species found in association with chinkapin oak include flowering dogwood *(Cornus florida)*, sassafras *(Sassafras albidum)*, sourwood *(Oxydendron arboreum)*, eastern hophornbeam *(Ostrya virginiana)*, *Vaccinium* spp., *Viburnum* spp., hawthorns *(Crataegus* spp.), and sumacs *(Rhus* spp.). The most common woody vines are wild grape *(Vitis* spp.) and greenbrier *(Smilax* spp.).

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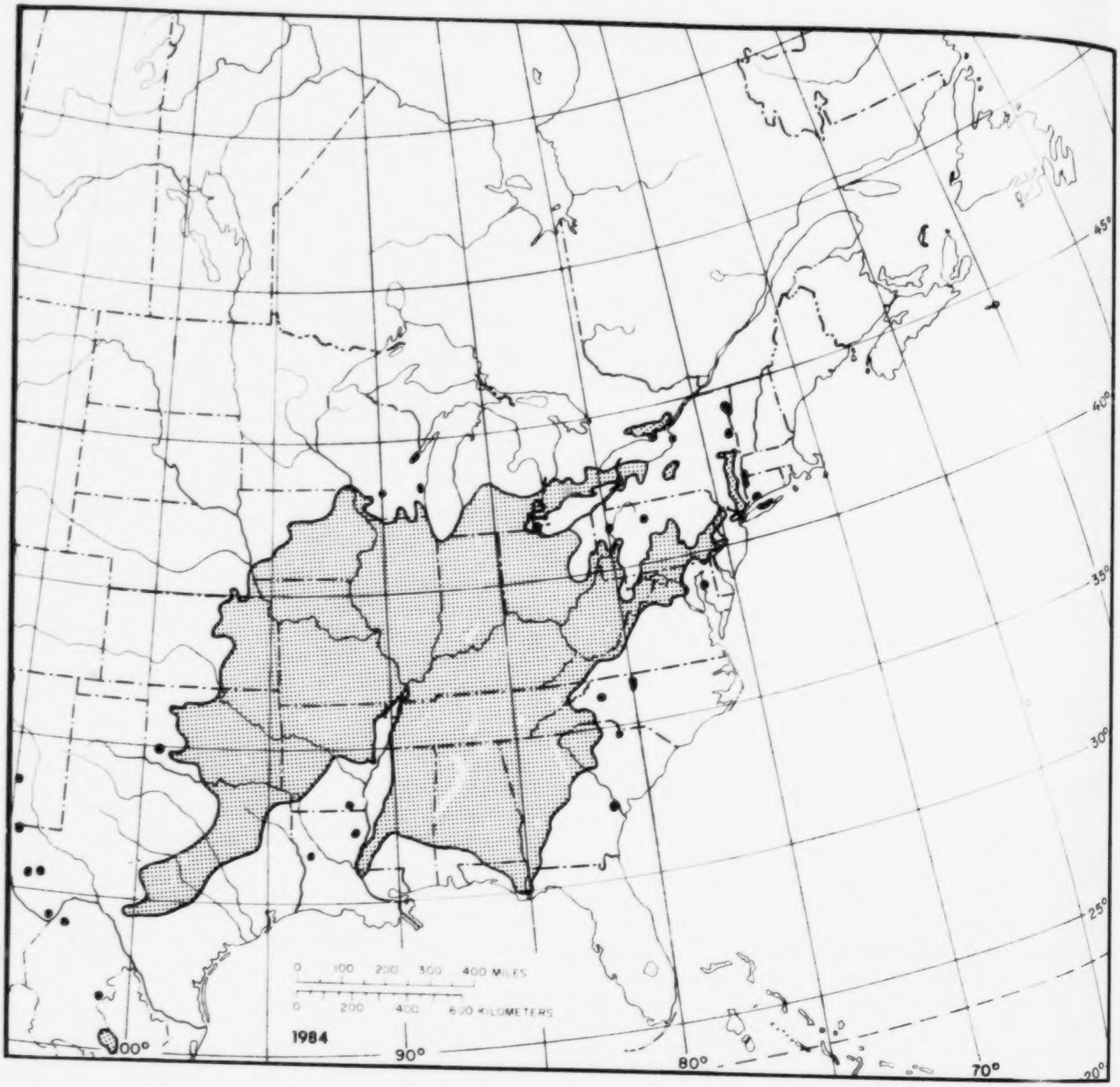

Figure 1—*The native range of chinkapin oak.*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Chinkapin oak is monoecious in flowering habit; flowers emerge in April to late May or early June. The staminate flowers are borne in catkins that develop from the leaf axils of the previous year, and the pistillate flowers develop from the axils of the current year's leaves. The fruit, an acorn or nut, is borne singly or in pairs, matures in 1 year, and ripens in September or October. About half of the acorn is enclosed in a thin cup and is chestnut brown to nearly black *(8)*.

Seed Production and Dissemination—Because chinkapin oak is not common, its seed production characteristics have not been studied. Observations in the Central States indicate, however, that good seed crops occur at infrequent intervals. Chinkapin oak acorns are disseminated in the same manner as those of other oaks—by gravity and rodents (*4*).

Seedling Development—Studies of oak regeneration in the Central States indicate chinkapin oak seedlings are established and grow much as do other upland oaks (*4,7*). Germination is hypogeal (*8*). Chinkapin oak acorns germinate in the fall soon after falling, and growth of the radicle continues until stopped by cold temperatures. Growth is resumed when the soil warms enough in the spring, at which time the epicotyl emerges. A light to moderate litter cover does not hinder germination and seedling establishment. Chinkapin oak seedlings tolerate moderate overstory or understory cover but growth is slow. When an old stand is harvested, the species must be present as large advance reproduction if it is to be a component of the new stand.

Vegetative Reproduction—Chinkapin oak sprouts readily and like other oaks the tops of advance reproduction generally are younger than the roots. Stumps of cut trees also sprout but no relation between sprouting frequency and stump size or age has been determined (*7*).

Rooting of stem cuttings and budding techniques have not been successful in propagating chinkapin oak, but some success has been attained with grafting (*4*).

Sapling and Pole Stages to Maturity

Growth and Yield—Chinkapin oak attains a height of from 18 to 24 m (60 to 80 ft) and a d.b.h. of from 61 to 91 cm (24 to 36 in) at maturity. In forest stands it develops a straight columnar bole with a dense rounded crown and fairly small branches; in the open it develops a short bole with a broad spreading crown.

Because chinkapin oak is usually found as scattered individuals, its growth characteristics have not been extensively studied. Observations from studies in the Central States, particularly southern Indiana, indicate its growth is similar to that of white oak on similar sites (*4*). It should respond well to release and there is no reason to discriminate against it in thinnings.

Rooting Habit—No information available.

Reaction to Competition—Chinkapin oak is classed as intolerant of shade. It withstands moderate shading when young but becomes more intolerant of shade with age. It is regarded as a climax species on dry, droughty soils, especially those of limestone origin. On more moist sites it is subclimax to climax. It is often found as a component of the climax vegetation in stands on mesic sites with limestone soils. However, many oak-hickory stands on moist sites that contain chinkapin oak are succeeded by the climax beech, maple, and ash (*1,4*).

Damaging Agents—Severe wildfire kills saplings and small pole-size trees but these resprout. Fire scars serve as entry points for decay-causing fungi, however, and the resulting decay can cause serious losses.

Oak wilt (*Ceratocystis fagacearum*), a vascular disease, attacks chinkapin oak and usually kills the tree within 2 to 4 years. Other diseases that attack chinkapin oak include the cankers *Strumella coryneoidea* and *Nectria galligena*, shoestring root rot (*Armillarea mellea*), anthracnose (*Gnomonia veneta*), and leaf blister (*Taphrina* spp.) (*4*).

The most serious defoliating insects that attack chinkapin oak are the gypsy moth (*Lymantria dispar*), the orangestriped oakworm (*Anisota senatoria*), and the variable oakleaf caterpillar (*Heterocampa manteo*). Insects that bore into the bole and seriously degrade the products cut from infested trees include the carpenterworm (*Prionoxystus robiniae*), little carpenterworm (*P. macmurtrei*), white oak borer (*Goes tigrinus*), Columbian timber beetle (*Corthylus columbianus*), oak timberworm (*Arrhenodes minutus*), and twolined chestnut borer (*Agrilus bilineatus*). The acorn weevils (*Curculio* spp.), larvae of moths (*Valentinia glandulella* and *Melissopus latiferreanus*), and gallforming cynipids (*Callirhytis* spp.) attack and destroy the acorns (*4*).

Special Uses

Chinkapin oak acorns are sweet and palatable and are eaten by squirrels, mice, voles, chipmunks, deer, turkey, and other birds. Acorns may be taken from the tree or from the ground. Because trees are scattered, chinkapin oak acorns are an important source of food only to the extent they contribute to the total mast available (*4*).

Genetics

Chinkapin oak intergrades with dwarf chinkapin oak (*Quercus prinoides*) and both have been recognized as varieties of the same species by some authors. Dwarf chinkapin oak, however, is commonly a low-growing, clump-forming shrub, rarely treelike, and is a separate distinct species.

Two recognized, named hybrids of chinkapin oak are *Q.* × *introgressa* P. M. Thomson (*Q. muehlenbergii* × *Q. bicolor* × *prinoides*), and *Q.* × *deamii* Trel. (*Q. muehlenbergii* × *macrocarpa*).

Chinkapin oak is also known to hybridize with white oak (*Q. alba*); Gambel oak (*Q. gambelii*); and dwarf chinkapin oak (*Q. prinoides*) (6).

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Quercus nigra L. Water Oak

Fagaceae Beech family

J. A. Vozzo

Water oak (*Quercus nigra*), sometimes called possum oak or spotted oak, is commonly found along southeastern watercourses and lowlands on silty clay and loamy soils. This medium-sized rapid-growing tree is often abundant as second growth on cutover lands. It is also planted widely as a street and shade tree in southern communities.

Habitat

Native Range

Water oak (figs. 1, 2) is found along the Coastal Plain from southern New Jersey and Delaware south to southern Florida; west to eastern Texas; and north

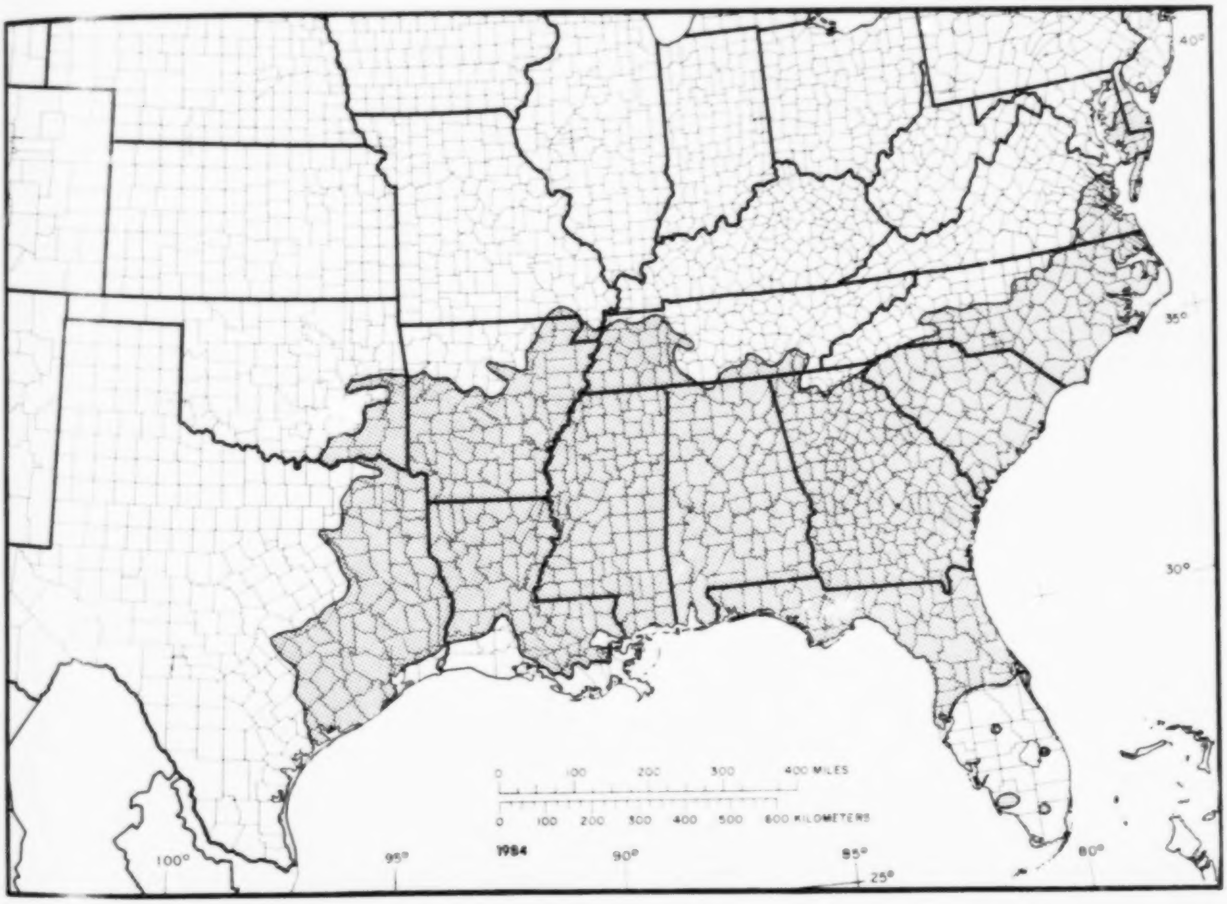
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Figure 1—*The native range of water oak.*

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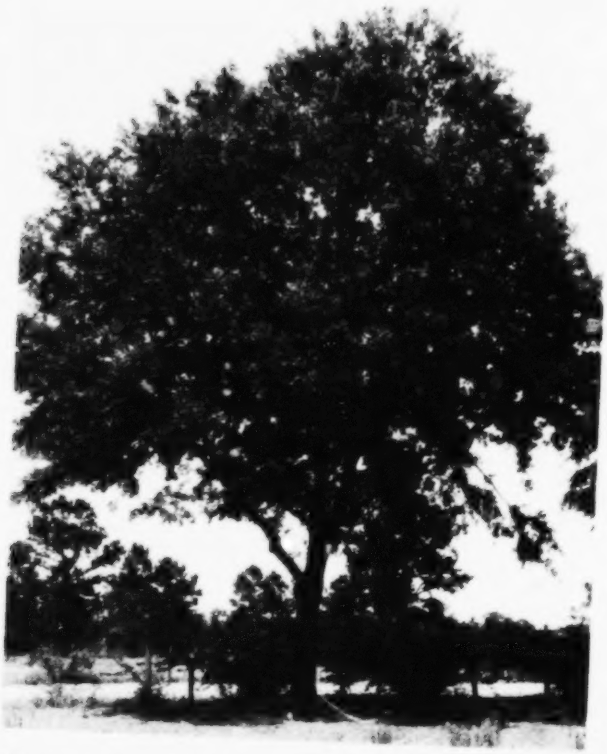

Figure 2—*Water oak.*

in the Mississippi Valley to southeastern Oklahoma, Arkansas, Missouri, and southwestern Tennessee *(3)*.

Climate

Water oak grows well along small streams or moist upland soils with 1270 to 1520 mm (50 to 60 in) annual rainfall during the frost-free period. Annual snowfall over the range varies from 0 to 50 cm (0 to 20 in) with 200 to 260 frost-free days. Summers of the southern-central range are warm and dry. July high temperatures vary from 21° to 46° C (70° to 115° F) and January low temperatures from 2° to -29° C (35° to -20° F) *(7)*.

Soils and Topography

Water oak appears on a wide variety of sites ranging from wet bottom lands to well-drained uplands. Best development and highest quality are found on the better-drained silty clay or loamy soils on high flats or ridges of alluvial stream bottoms. Water oaks are commonly found on soils of the order Inceptisols *(9)*. On low flats with poorly drained clay soils, tree form and quality are poor. Water oak can survive on moist upland sites.

Associated Forest Cover

Water oak is associated with the following tree species: willow oak *(Quercus phellos)*, laurel oak *(Q. laurifolia)*, Nuttall oak *(Q. nuttallii)*, cherrybark oak *(Q. falcata)*, white oak *(Q. alba)*, swamp chestnut oak *(Q. michauxii)*, American beech *(Fagus grandifolia)*, sweetgum *(Liquidambar styraciflua)*, pecan *(Carya illinoensis)*, American elm *(Ulmus americana)*, slippery elm *(U. rubra)*, winged elm *(U. alata)*, blackgum *(Nyssa sylvatica)*, green ash *(Fraxinus pennsylvanica)*, white ash *(F. americana)*, yellow-poplar *(Liriodendron tulipifera)*, southern magnolia *(Magnolia grandiflora)*, flowering dogwood *(Cornus florida)*, roughleaf dogwood *(C. drummondii)*, honeylocust *(Gleditsia triacanthos)*, Carolina laurelcherry *(Prunus caroliniana)*, hawthorn *(Crataegus* spp.), American hornbeam *(Carpinus caroliniana)*, sugarberry *(Celtis laevigata)*, swamp privet *(Forestiera acuminata)*, as well as several softwoods including spruce pine *(Pinus glabra)*, loblolly pine *(P. taeda)*, longleaf pine *(P. palustris)*, and slash pine *(P. elliottii) (6)*.

Water oak is classified as a bottom-land forest cover type Willow Oak–Water Oak–Diamondleaf Oak (Society of American Foresters Type 88) *(6)*. It is also an associated species in Live Oak (Type 89) and Sweetbay–Swamp Tupelo–Redbay (Type 104).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Water oak is monoecious; staminate flowers are in hanging catkins and pistillate flowers are in few-flowered, short-stalked clusters on the same tree. They develop shortly before or at the same time as the new leaves. Staminate flowers are produced near the tip of the previous year's growth, while pistillate flowers are produced in the junction of the current year's growth *(5)*. The fruit, an acorn, matures about September of the second year. The embryo has no endosperm but two large, fleshy cotyledons *(4)*.

Flowers are easily killed by late frosts after leaf buds open. The trees then defoliate and develop new leaves but do not generate a second crop of flowers.

Seed Production and Dissemination—Trees bear seed at about age 20 and production seems to alternate between prolific and lean years. Mature trees yield 9 to 53 liters (0.25 to 1.5 bu) of acorns in a good year, with about 64.4 kg/ha (50 lb/bu). The average for cleaned seeds is 880/kg (400/lb) *(4)*. Generally, viable acorns sink in water, while those that float probably will not germinate. Water oak acorns are naturally disseminated by animals and water.

Seedling Development—Under controlled conditions, water oak acorns require a pregermination treatment to overcome dormancy. Under natural conditions, they germinate the spring following maturation. They may be induced to germinate by stratification for 30 to 40 days in moist sand at 30° to 32° C (86° to 90° F) during light cycles and for a 52- to 73-day period at 20° to 21° C (68° to 70° F) during dark cycles. Expect 60 to 94 percent germination after 31 to 73 days. Germination is hypogeal *(4)*.

Seedlings require abundant moisture the entire growing season but do not tolerate prolonged submersion. Under optimum conditions water oak grows at a rate of 60 cm (24 in) per year for the first 25 years *(7)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Water oak can grow to 38 m (125 ft) on a site index range of 18.3 to 33.5 m (60 to 110 ft) at base age 50 years *(1)*. It prunes itself slowly, developing a straight, slender main trunk. Growing quickly on favorable sites, it can produce 15 to 30 cm (6 to 12 in) of d.b.h. growth in 10 years. It can grow 7.8 cm (3.1 in) in d.b.h. in 10 years while in the 36 to 46 cm (14 to 18 in) diameter class; and 7.4 cm (2.9 in) in the 51 to 71 cm (20 to 28 in) class *(7)*. Water oak has a shallow, spreading rooting habit.

Rooting Habit—No information available.

Reaction to Competition—Water oak does not compete well with other species because of its slow early growth and its intolerance to shade and competition. It is a subclimax tree. Water oak germinates under shade, but seedlings require moderate light for development. Epicormic branching is common for water oak in suppressed to intermediate crown position. Stumps will sprout, but vegetative propagation is not economically practical as a management procedure *(7)*.

Water oak is easily injured by fire and even a light burn kills stems of seedlings. Survivors are extremely susceptible to butt rot.

Damaging Agents—Natural enemies of water oak are primarily insects and microorganisms *(2,7,8)*. Insects include trunk borers *(Enaphalodes* sp. and *Prionoxystus* sp.) and leaf hoppers *(Erythroneura* sp.). The more noticeable diseases include cone rusts *(Cronartium* spp.), root rot *(Ganoderma curtisii)*, and trunk canker and heart rot caused by a variety of organisms. Additionally, water oak is susceptible to parasitism by mistletoe *(Phoradendron flavescens)*. Herbicides such as 2,4,5-T and picloram compounds are toxic to water oak. It is also highly susceptible to air pollution, probably to sulfur dioxide in particular.

Special Uses

Water oak is particularly suited for timber, fuel, wildlife habitat, and environmental forestry *(4)*. It has been widely planted in southern communities as a shade tree. Its veneer has been successfully used as plywood for fruit and vegetable containers *(8)*.

Genetics

There are no reported racial variations of water oak. It hybridizes with other oak species as follows *(3)*: *Quercus falcata* (*Q.* × *garlandensis* Palmer), *Q. incana* (*Q.* × *caduca* Trel.), *Q. laevis* (*Q.* × *walteriana* Ashe), *Q. marilandica* (*Q.* × *sterilis* Trel.), *Q. phellos* (*Q.* × *capesii* W. Wolf), *Q. shumardii* (*Q.* × *neopalmeri* Sudw.), and *Q. velutina* (*Q.* × *demarei* Ashe).

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Quercus nuttallii Palmer **Nuttall Oak**

Fagaceae **Beech family**

T. H. Filer, Jr.

Nuttall oak (*Quercus nuttallii*), not distinguished as a species until 1927, is also called red oak, Red River oak, and pin oak. It is one of the few commercially important species found on poorly drained clay flats and low bottoms of the Gulf Coastal Plain and north in the Mississippi and Red River Valleys. The acorn or winter buds identify Nuttall oak, easily confused with pin oak (*Q. palustris*). The lumber is often cut and sold as red oak. In addition to producing timber, Nuttall oak is an important species for wildlife management because of heavy annual mast production.

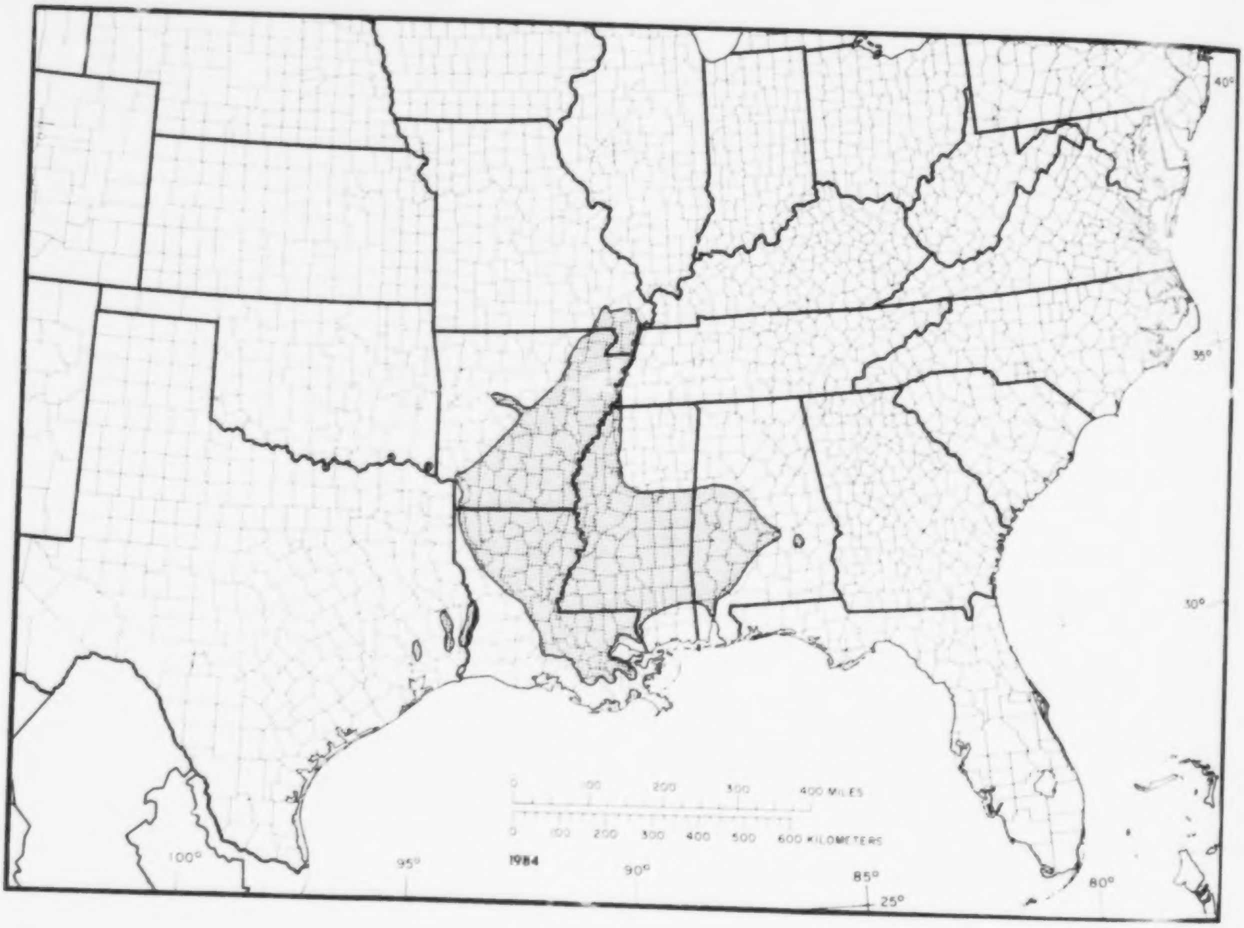

Figure 1—*The native range of Nuttall oak.*

The author is Principal Plant Pathologist, Southern Forest Experiment Station, New Orleans, LA.

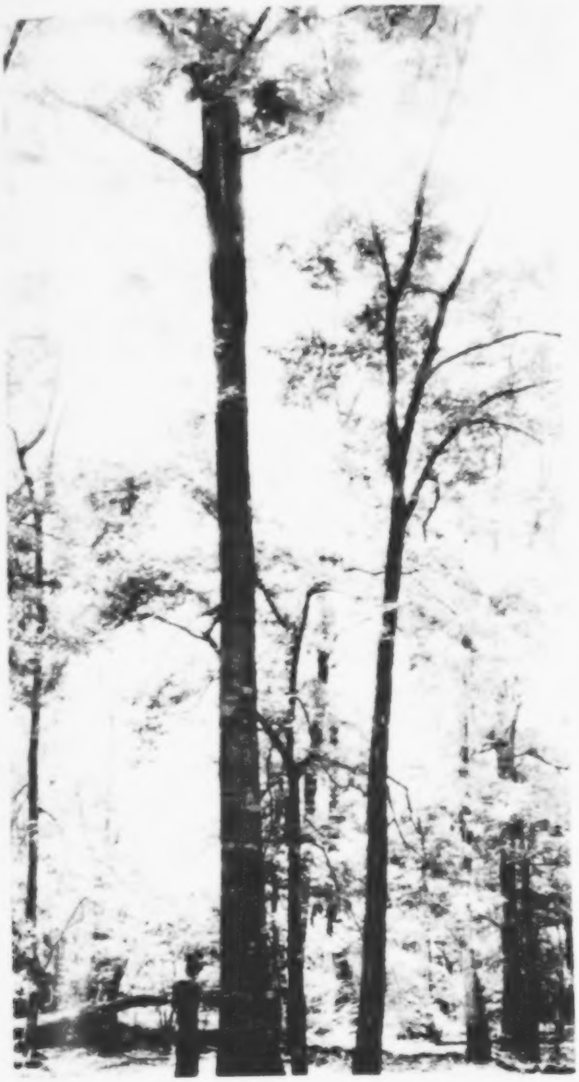

Figure 2—*Nuttall oak growing on Dowling clay soil on the Tallahatchie National Forest in Mississippi.*

Habitat

Native Range

Nuttall oak (fig. 1) grows on bottom lands along the Gulf Coastal Plain from Florida west to southeastern Texas. North in the Mississippi Valley, it is found in Arkansas, southeastern Oklahoma, southeastern Missouri, and western Tennessee. It develops best on the alluvial bottom lands of the Mississippi River and its tributaries.

Climate

The climate throughout the range of Nuttall oak is humid. Rainfall is between 1270 to 1650 mm (50 to 65 in) per year; 630 to 760 mm (25 to 30 in) fall during the effective growing season, April through August. At the northern limits of the range, 2.5 to 12.5 cm (1 to 5 in) of the total precipitation falls as snow. Maximum summer temperature averages 27° C (80° F) while the winter average varies from 7° to 13° C (45° to 55° F). The extreme high and low temperatures are 43° to -26° C (110° to -15° F) *(23)*.

Soils and Topography

Nuttall oak grows well on heavy, poorly drained, alluvial clay soils in the first bottoms of the Mississippi Delta region (fig. 2) *(17,24)*, performing best on soils with a pH of 4.5 to 5.5 *(1,7)*. It is common on clay ridges but is not found in permanent swamps or on well-drained loam. Typically, it grows on clay flats that are normally covered with 8 to 20 cm (3 to 8 in) of water throughout the winter. The tree is less common on clay or silty clay flats and sloughs on the terrace of major streams. In the Coastal Plain, Nuttall oak grows mostly in alluvial river bottoms on sites similar to those described for the Delta *(24)*. In general, Nuttall oak grows on soils primarily in the orders Inceptisols and Entisols.

Associated Forest Cover

Nuttall oak is a chief component of the forest cover type Sweetgum–Willow Oak (Society of American Foresters Type 92) *(8)*. Water oak replaces willow oak (*Q. phellos*) in the southernmost part of the type's range. The species is found in five other types: Sugarberry–American Elm–Green Ash (Type 93), Sycamore–Sweetgum–American Elm (Type 94), Overcup Oak–Water Hickory (Type 96), Baldcypress (Type 101), and Baldcypress–Tupelo (Type 102).

Other trees associated with Nuttall oak are cedar elm (*Ulmus crassifolia*), laurel oak (*Quercus laurifolia*), bur oak (*Q. macrocarpa*), red and silver maple (*Acer rubrum* and *A. saccharinum*), black willow (*Salix nigra*), honeylocust (*Gleditsia triacanthos*), and persimmon (*Diospyros virginiana*).

Noncommercial tree and shrub associates are roughleaf dogwood (*Cornus drummondii*), hawthorn (*Crataegus* spp.), swamp-privet (*Forestiera* *acuminata)*, buttonbush *(Cephalanthus occidentalis)*, and water-elm *(Planera aquatica) (24)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Nuttall oak is monoecious. The male and female flowers appear in March and April at the time of leaf flushing. The male flower appears 10 to 14 days before the female flower. Male flowers are borne in clustered, yellowish-green catkins. Inconspicuous female flowers are borne in the axils of the new leaves and are found only by close examination. The flowers are wind pollinated. The acorns ripen from September to October of the second year and fall between September and February.

Seed Production and Dissemination—Young trees about 20 years old produced good seed crops for several years at Stoneville, MS; this is probably the age at which optimum seed-bearing begins. In the TVA arboretum at Norris, TN, 5-year-old trees bore acorns. There are generally good seed crops every 3 or 4 years, and the average tree yields 6 to 35 kg (13 to 77 lb) of clean nuts in 9 to 53 liters (0.25 to 1.5 bushels). The nuts average 209/kg (95/lb) *(27)*. Water, rodents, and birds disseminate the seed.

Seedling Development—Nuttall oak seeds require 60 to 90 days cold stratification. They overwinter and germinate in the spring when soil temperatures are 21° to 32° C (70° to 90° F) *(27)*. Seed germination percentages average 60 to 90 percent but germination varies by size and may be reduced by acorn weevil damage. Larger acorns had somewhat higher germination rates than smaller ones. The percent of germination was unaffected even when seeds were submerged in water for as long as 34 days *(5)*. Germination is hypogeal *(27)*. The best natural seedbed for most Nuttall oaks is a moist soil, covered with an inch or more of soil or leaf litter with partial shade *(12)*.

Although rodents, turkeys, deer, and hogs eat many of the seeds, natural reproduction in the bottom lands is usually abundant. Seedlings are often killed by high water during the growing season, but seedling survival, date of budbreak, or height growth are not significantly affected. When grown in saturated soil for 16 weeks in winter and spring *(3)*, Nuttall oak seedlings become established both in the open or in shade, and can survive 5 to 10 years in the shade *(15)*. Strong tap roots are developed *(13)*. Mycorrhizal roots were common on seedlings growing in green-tree reservoir plots *(9)*.

Vegetative Reproduction—Methods for propagating Nuttall oak from cuttings or by grafting have not been developed. When attempted, air-layering has not been successful *(2)*. Stumps of small trees sprout readily, but those of older trees do not.

Sapling and Pole Stages to Maturity

Growth and Yield—Nuttall oak grows rapidly with a 5-year average of 4.08 m (13.4 ft) height growth and 0.006 m^3 (0.2 ft^3) increase in stem volume *(17,18,19)*. Second-growth trees reach a merchantable size, 60 cm (24 in) in d.b.h. in about 70 years. Trees 30 to 37 m (100 to 120 ft) tall and 90 cm (36 in) and larger in d.b.h. are common in old stands, but even trees of good quality degenerate rapidly soon after they mature.

A 10 cm (4 in) diameter growth in 10 years is common but 20 cm (8 in) is possible. By impounding winter and spring rainfall, radial tree growth was increased by about 38 percent as compared to that of untreated trees *(6)*.

On poor sites the wood of this oak is knotty, and insect damage and mineral stain are severe. Several successive years of drought and channelization of waterways may lower the water table on what normally would be good Nuttall oak sites and cause trees of all ages to die *(24)*.

Rooting Habit—No information available.

Reaction to Competition—Nuttall oak is classed as intolerant of shade; seedlings survive and grow rapidly only in openings. The tree is almost always dominant or codominant *(13,14,16)*.

Damaging Agents—Acorn weevils *(Curculio* spp.) can reduce acorn germination by causing damage to developing acorns. The carpenterworm *(Prionoxystus robinise)* causes heavy damage to Nuttall oak. Other borers that cause timber defects are the red oak borer *(Enaphalodes rufulus)*, the white oak borer *(Goes tigrinus)*, others of the genus *Goes*, the oak sapling borer *(G. tesselatus)*, and the hardwood stump borer *(Stenodontes dasytomus)*. The clearwing borer *(Paranthrene simulans)* creates an entry point for rot and stain fungi, causing additional defects. Estimated loss from borer defects in oak lumber is approximately $40 million per year *(25)*. Other borers infect twigs, branches and roots, reducing growth and vigor, but do no damage to the merchantable parts of the tree.

A serious insect-caused defect in Nuttall oak lumber is bark pocket caused by the sap-feeding beetles *(nitidulids)* in combination with the carpenterworm and several other borers *(22)*. Periodic outbreaks of defoliating insects such as basswood leafminer *(Baliosus nervosus)* and pink striped oakworm *(Anisota virginiensis)* retard growth rates of oaks over large geographical areas *(26)*.

Nuttall oak is subject to attack by three important canker rot fungi. All enter the trunk through dead branch stubs by germination of airborne spores. The cambium is killed, rough cankers are induced around the entry point, and the heartwood is decayed. The resulting cankers are called hispidus, spiculosa, or Irpex, depending on the causal fungi—*Polyporus hispidus, Poria spiculosa,* and *Spongipellis pachyodon* respectively *(21)*. Nuttall oak growing north of 35° latitude may be killed by oak wilt *(Ceratocystis fagacearum)*. Daily temperatures above 30° C (86° F) reduce development of the disease *(20)*.

Anthracnose *(Gnomonia quercina)* and Actinopelte leaf spot *(Actinopelte dryina)* cause defoliation in some years *(26)*.

Special Uses

Nuttall oak is an important species in green-tree reservoirs, where ducks feed on the acorns *(10)*. Acorns contain 13 percent crude fat and 46 percent carbohydrates *(4)*. In Louisiana, it is considered one of the best mast-producing species. Acorn crops rarely fail *(11)*.

During periods of winter flooding, squirrels find a ready supply of acorns, since many acorns remain on the tree into January. Acorns are favored by deer and also eaten by turkeys.

Genetics

No racial variations or hybrids have been reported. North of Memphis, TN, this tree is easily confused with *Q. palustris* (pin oak).

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Quercus palustris Muenchh. Pin Oak

Fagaceae Beech family

Robert A. McQuilkin

Pin oak *(Quercus palustris)*, also called swamp oak, water oak, and swamp Spanish oak, is a fast-growing, moderately large tree found on bottom lands or moist uplands, often on poorly drained clay soils. Best development is in the Ohio Valley.

The wood is hard and heavy and is used in general construction and for firewood. Pin oak transplants well and is tolerant of the many stresses of the urban environment, so has become a favored tree for streets and landscapes.

Habitat

Native Range

Pin oak (figs. 1, 2) grows from southwestern New England west to extreme southern Ontario, southern Michigan, northern Illinois, and Iowa; south to Missouri, eastern Kansas, and northeastern Oklahoma; then east to central Arkansas, Tennessee, central North Carolina, and Virginia *(16)*.

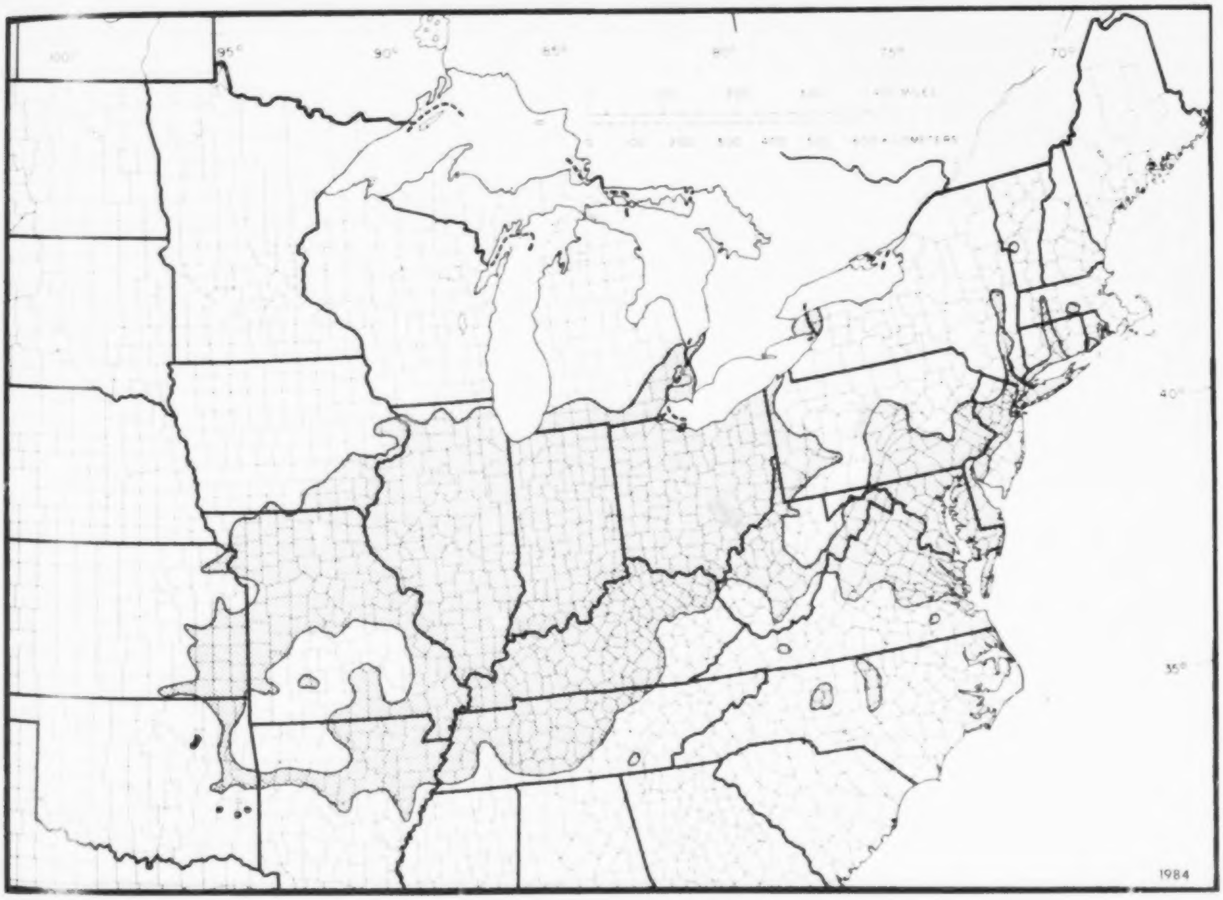

Figure 1—*The native range of pin oak.*

The author is Forester, USDA Forest Service, Northeastern Area State and Private Forestry, Radnor, PA.

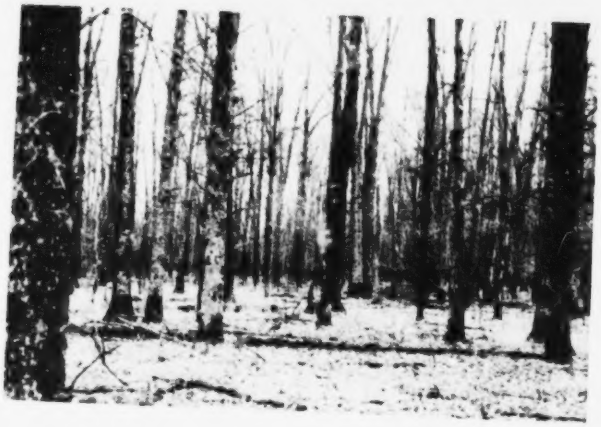

Figure 2—*A 55-year-old pin oak stand on a poorly drained bottom land in southeastern Missouri. Note the many dead branches on the lower boles, and the discoloration on the base of the trees indicating the flooding level the previous winter.*

Climate

The climate throughout most of the range of pin oak is classified as humid or, in the northwestern portion, moist subhumid. Precipitation varies from 810 mm (32 in) along the western and northern edges of the pin oak range to more than 1270 mm (50 in) in Arkansas and Tennessee. Mean annual temperatures and growing season lengths range from 10° C (50° F) and 120 days in southern New England to 16° C (60° F) and more than 210 days in northern Arkansas and western Tennessee *(16)*.

Soils and Topography

Pin oak grows primarily on level or nearly level, poorly drained alluvial floodplain and river bottom soils with high clay content (order Entisols). Pin oak is usually found on sites that flood intermittently during the dormant season but do not ordinarily flood during the growing season. It does not grow on the lowest, most poorly drained sites that may be covered with standing water through much of the growing season. It does grow extensively on poorly drained upland "pin oak flats" on the glacial till plains of southwestern Ohio, southern Illinois and Indiana, and northern Missouri (order Alfisols). Because of the level topography and presence of a claypan in the soil, these sites tend to be excessively wet in the winter and spring *(22)*.

Associated Forest Cover

Pin oak is a major species in only one forest cover type, Pin Oak–Sweetgum (Society of American Foresters Type 65), which is found on bottom lands and some upland sites throughout the central portion of the pin oak range *(8)*. Associated species in this type include red maple *(Acer rubrum)*, American elm *(Ulmus americana)*, black tupelo *(Nyssa sylvatica)*, swamp white oak *(Quercus bicolor)*, willow oak *(Q. phellos)*, overcup oak *(Q. lyrata)*, bur oak *(Q. macrocarpa)*, green ash *(Fraxinus pennsylvanica)*, Nuttall oak *(Quercus nuttallii)*, swamp chestnut oak *(Q. michauxii)*, and shellbark *(Carya laciniosa)* and shagbark *(C. ovata)* hickories. Pin oak and sweetgum *(Liquidambar styraciflua)* vary in their relative proportions in this cover type, and large areas of almost pure pin oak occur on the "pin oak flats" of the upland glacial till plains or in the bottom lands of the lower Ohio and central Mississippi River valleys.

Pin oak is an associated species in Silver Maple–American Elm (Type 62) in the bottom lands along the Ohio, Wabash, Mississippi, and Missouri Rivers; a variant of this type, silver maple–American elm–pin oak–sweetgum, is found along major streams in southern Illinois and Indiana.

Pin oak also occurs in Black Ash–American Elm–Red Maple (Type 39) in poorly drained bottom lands in northern Ohio and Indiana along with silver maple *(Acer saccharinum)*, swamp white oak, sycamore *(Platanus occidentalis)*, black tupelo, and eastern cottonwood *(Populus deltoides)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pin oak is monoecious; flowers appear at about the time the leaves develop in the spring. Staminate flowers are borne on aments that develop from buds formed in the leaf axils of the previous year, and pistillate flowers are borne on short stalks from the axils of current-year leaves. Pollination is by wind. Fruit is an acorn (nut) that matures at the end of the second growing season after flowering. Acorns are dispersed from September to early December *(25)*.

Seed Production and Dissemination—Pin oak stands begin producing seed at about age 20, but open-grown trees may begin at ages as young as 15 years *(22,25)*.

During a 14-year period, production of mature acorns in 32- to 46-year-old pin oak stands in southeastern Missouri averaged 210,300/ha (85,100/acre) but varied yearly from 13,300 to 492,700/ha (5,400 to 199,400/acre). Poor acorn crops occurred at 3- to 4-year intervals. Insect infestation rates varied inversely with crop size and, over all years, averaged 26 percent *(19)*.

Pin oak acorns are dispersed by squirrels, mice, blue jays, and woodpeckers.

Pin oak acorns submerged in cold water as long as 6 months were not damaged. This tolerance may be partly due to a thick, waxy coating on the pericarp that impedes water absorption *(5,23)*.

The acorns require stratification of 30 to 45 days at 0° to 5° C (32° to 41° F) to break dormancy, and germination of sound, stratified acorns averages about 68 percent *(30)*.

Seedling Development—Germination is hypogeal *(22)*. Pin oak seedlings established after good seed years are often abundant. In southeastern Missouri, an average of 8,650 new seedlings per hectare (3,500/acre) were present the summer following a good seed year. Seedling establishment rates were higher on areas that had been scarified the previous summer than on undisturbed areas. In an adjacent area that had been artificially flooded for 3 months during the winter, almost no new seedlings developed, partly because many of the acorns were consumed by thousands of migrating ducks attracted to the flooded area during the winter *(23)*.

Although large numbers of seedlings can become established after good seed years, under fully stocked stands most die within 5 years because of their shade intolerance. Even under these conditions, however, a few individuals may live as long as 30 years, although they grow very slowly and frequently die back and resprout *(22)*.

When established first-year seedlings are subjected to shallow flooding (tops and leaves above water) during the growing season, root growth ceases, some secondary roots die, and almost no adventitious roots are formed. Although growth during flooding is poor and recovery after flooding may be slow, seedling survival to such shallow flooding for as long as 84 days is high *(7)*. Pin oak seedlings survive complete inundation (tops and leaves under water) for only 10 to 20 days during the growing season. They are classified as intermediate in tolerance to growing season shallow flooding along with cottonwood, sycamore, and silver maple; but they are less tolerant than water tupelo *(Nyssa aquatica)*, green ash, and black willow *(Salix nigra) (13,14)*. Neither shallow flooding nor complete inundation during the dormant season has an adverse effect on pin oak seedlings *(4)*.

Vegetative Reproduction—Pin oak sprouts vigorously from stumps of young trees, and, if the origin of the sprouts is low on the stump, the incidence of decay from the parent stump is low. After physiological die-back or injury to the top, young seedlings sprout readily from dormant buds on the stem or root collar *(22)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Pin oak grows rapidly. In well-stocked, even-aged bottomland stands in southeastern Missouri, pin oak crop trees averaged 28 cm (11 in) in d.b.h. and 20 m (65 ft) in height at age 30, and more than 40 cm (16 in) in d.b.h. at age 50. On good bottomland sites, stands normally reach heights of 24 to 27 m (80 to 90 ft) and diameters of approximately 60 cm (24 in) by 75 years, and individual trees may eventually attain heights of 37 m (120 ft) and diameters of 150 cm (60 in) *(22,26)*.

Pin oak responds rapidly to thinning. After release, pin oak crowns expand quickly to occupy the additional growing space, and diameter growth increases rapidly. Net annual growth on plots thinned at age 37 in southern Illinois was 8.8 m^3/ha (125 ft^3/acre). At age 40 these stands had 42.0 m^3/ha (3,000 fbm/acre) in trees 27 cm (10.6 in) in d.b.h. and larger and were growing at a rate of 4.2 m^3 to 7.0 m^3/ha (300 to 500 fbm/acre) per year. Typical 60- to 70-year-old bottomland pin oak stands yield 112 to 168 m^3/ha (8,000 to 12,000 fbm/acre) of merchantable sawtimber. Growth of pin oaks on upland till-plain sites is much less than on bottom-land sites *(22)*.

Pin oak is a short-lived species and reaches physiological maturity at 80 to 100 years. Little is known about maximum ages attained, but in one old-growth stand in Kentucky trees averaged 138 years of age *(6,22)*.

Pin oak is strongly excurrent in growth form, and even open-grown trees maintain a well-defined main trunk through most of the crown (fig. 3). Trees grown in forest stands have narrow crowns, but open-grown trees develop wide, symmetrical crowns in which the upper branches bend upward, the midcrown branches are horizontal, and the lower branches bend downward. This characteristic branching habit gives the tree a distinctive pyramidal shape.

Pin oak is not self-pruning. Many of the lower bole branches remain alive on open-grown trees, and although most of these branches die in closed stands, the dead branches are retained for many years. This characteristic causes many small "pin knots" in the lumber and gives the species its common name. (Some authorities ascribe the derivation of the common name to the prevalence of short, pinlike branches on the main lateral limbs *(11)*.) Pruning removes these lower branches, but its benefit is partially offset by the subsequent development of new

Figure 3—*Pin oak.*

epicormic sprouts. Twelve years after the first 4.9-m (16-ft) log was pruned on 30-year-old trees in even-aged stands in southeastern Missouri, pruned trees have less than one-fourth as many branches as unpruned trees (6.1 compared to 25.6 branches) *(18)*.

Rooting Habit—In well-aerated soils, pin oak seedlings initially develop a strong taproot. As the trees become older, however, the root system loses this configuration and becomes more fibrous. When transplanted, bare-root seedlings and small saplings of pin oak quickly regenerate an extensive, fibrous root system *(7,24)*.

Reaction to Competition—Pin oak is classed as intolerant of shade. It is less tolerant than elm, boxelder *(Acer negundo)*, sweetgum, hackberry *(Celtis occidentalis)*, and ash but is more tolerant than eastern cottonwood and black willow. Pin oak usually grows in even-aged stands of dominant and codominant trees; intermediate and suppressed trees in such stands usually die within a few years of being overtopped. Single pin oaks in mixed stands usually are dominants. Pin oak is considered a subclimax species; it persists, however, on heavy, wet soils because it produces an abundance of reproduction which, if released, grows faster on these sites than most of its competitors *(22,29)*.

Damaging Agents—Although pin oak is very tolerant of dormant-season flooding, it is much less tolerant of growing-season flooding and trees may be injured or killed by intermittent growing-season flooding over several successive years. The trees can usually survive one growing season of continuous flooding but will be killed by continuous flooding over 2 or 3 consecutive years *(2,4,10,22)*. Pin oak is rated as "intermediately tolerant" to growing season flooding, along with such species as sugar maple *(Acer saccharum)*, river birch *(Betula nigra)*, southern red oak *(Quercus falcata)*, and Shumard oak *(Q. shumardii)*; it is less tolerant than red maple, silver maple, sweetgum, sycamore, swamp white oak, and American elm (tolerant) and eastern cottonwood, green ash, and black willow (very tolerant) *(28,29)*.

Dormant-season flooding for 20 years in a greentree reservoir in southeastern Missouri did not appear to damage pin oak trees, but did reduce stand basal area growth by 10 percent *(26)*. However, in this same area approximately 5 years later (i.e., after 25 years of flooding), many of these trees had developed bole swellings at and just above the average flood water level. These swellings caused longitudinal fissures in the bark up to 10 cm (4 in) wide, thereby exposing the bole xylem to decay organisms. The cause of this phenomenon is unknown, but it appears to be associated with the continuous dormant-season flooding, because pin oaks in adjacent areas subject only to intermittent natural flooding were not similarly affected *(27)*.

The bark of pin oak is relatively thin and the species is therefore especially susceptible to damage by fire and the decay associated with fire wounds *(12,22)*.

Pin oak is subject to most of the diseases of oaks including oak wilt *(Ceratocystis fagacearum)* and is particularly susceptible to a leaf blister fungus *(Taphrina caerulescens)*, a shoot-blight and twig canker fungus *(Dothiorella quercina)*, and pin oak blight *(Endothia gyrosa) (12)*.

Pin oak is also host to many of the common oak-feeding insects including many defoliators, wood borers, gall wasps, and acorn weevils. Pin oak is classified as a "most preferred" host for gypsy moth *(Lymantria dispar) (15)*, and is also especially susceptible to the obscure scale *(Melanaspis obscura)*, oak leaftier *(Croesia semipurpurana)*, pin oak sawfly

(Caliroa lineata), scarlet oak sawfly *(C. quercuscoccineae)*, the sawfly *Calinoa petiolata*, the forest tent caterpillar *(Malacosoma disstria)*, a leafroller *(Argyrotaenia quercifoliana)*, the horned oak gall wasp *(Callirhytis cornigera)*, and the gouty oak gall wasp *(C. quercuspunctata)*. Thousands of acres of pin oak stands in southern Illinois have been severely damaged over the past 25 years by outbreaks of the horned oak gall wasp and the forest tent caterpillar *(1,31,32,33)*.

Ornamental pin oaks planted on alkaline soils often develop foliar chlorosis (yellowing) which, if severe, can kill the tree. This chlorosis was previously thought to be a simple iron deficiency, but recent research has indicated that it is a more complex phenomenon involving reduced foliar concentrations of one or more of the micronutrients Fe, Mn, or Zn, often in association with increased foliar concentrations of one or more of the macronutrients P, K, or Mg. In most cases, this problem can be easily corrected by soil applications of sulfuric acid. Chlorosis is not a problem in natural stands of pin oak which occur on more acidic soils *(20,21)*.

Special Uses

Pin oak acorns are an important food for mallards and wood ducks during their fall migration. Pin and other bottom-land oaks are the primary tree species in bottom-land duck-hunting areas (greentree reservoirs) that are artificially flooded during the fall and winter to attract migrating waterfowl *(19)*. Pin oak acorns are also an important food for deer, squirrels, turkeys, woodpeckers, and blue jays.

The wood of pin oak is similar to that of northern red oak, and pin oak lumber is marketed under the general designation of "red oak." The occurrence of numerous small knots in the wood of many pin oak trees limits its use for high quality products, however *(11)*.

Pin oak transplants well, and because of its rapid growth, large symmetrical crown, and scarlet fall colorations, it is commonly planted as a shade or ornamental tree *(24)*.

Genetics

No races or genetically distinct populations have been defined within pin oak, but the existence of such populations has been suggested based on differences in flood tolerance and resistance to iron chlorosis *(3,9)*.

Five hybrids of pin oak are recognized *(17)*: *Quercus* × *mutabilis* Palmer & Steyerm. *(Q. palustris* × *shumardii)*, *Q.* × *vaga* Palmer & Steyerm. *(Q. palustris* × *velutina)*, *Q.* × *schochiana* Dieck *(Q. palustris* × *phellos)*, *Q.* × *columnaris* Laughlin *(Q. palustris* × *rubra)*, and an unnamed hybrid with *Q. coccinea*.

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Quercus phellos L. Willow Oak

Fagaceae Beech family

Bryce E. Schlaegel

Willow oak *(Quercus phellos)*, also known as peach oak, pin oak, and swamp chestnut oak, grows on a variety of moist alluvial soils, commonly on lands along water courses.

This medium to large southern oak with willowlike foliage is known for its rapid growth and long life. It is an important source of lumber and pulp, as well as an important species to wildlife because of heavy annual acorn production. It is also a favored shade tree, easily transplanted and used widely in urban areas.

Habitat

Native Range

Willow oak (fig. 1) is found mainly in bottom lands of the Coastal Plain from New Jersey and

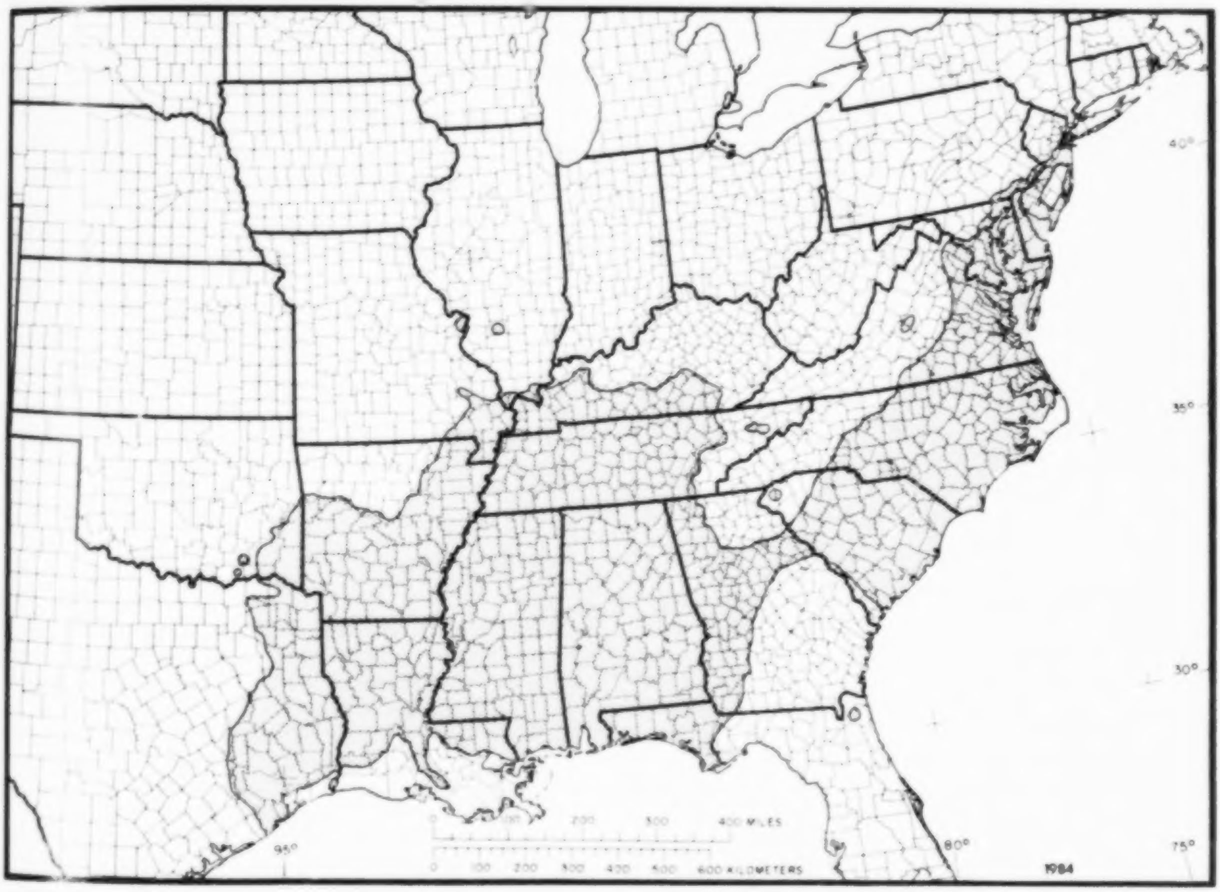

Figure 1.—*The native range of willow oak.*

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southeastern Pennsylvania south to Georgia and northern Florida; west to eastern Texas; and north in the Mississippi Valley to southeastern Oklahoma, Arkansas, southeastern Missouri, southern Illinois, southern Kentucky, and western Tennessee *(14)*.

Climate

The climate in which willow oak grows is humid and temperate, characterized by long, hot summers and mild, short winters. It grows mainly in the zone where daily normal temperatures are above 0° C (32° F). Frost-free days number 180 to 190 in the north-northeastern range and 300 in the south–southwestern range *(29)*. Average summer temperatures vary from 21° to 27° C (70° to 80° F), with extremes of 38° to 46° C (100° to 115° F). Average winter temperatures range from -4° to 13° C (25° to 55° F) with extremes to -29° C (-20° F). Average annual temperatures throughout the range are 10° to 21° C (50° to 70° F).

Across the entire range, surface winds in the summer are off the Gulf of Mexico and winter winds are variable. Normally there are about 2,700 hours of sunshine annually in willow oak's range. Relative humidity at noon ranges from 60 to 70 percent in January and 50 to 70 percent in July.

Annual precipitation varies from 1020 to 1520 mm (40 to 60 in) and is fairly evenly distributed throughout the year; there is slightly more precipitation in the summer in the southeastern portion of the range. Greatest precipitation is in the central Gulf area. Average annual snowfall varies from 0 to 127 cm (0 to 50 in) over the range. The normal number of days with snow cover of at least 2.5 cm (1 in) varies from 0 to 40.

Soils and Topography

Willow oak grows on a variety of alluvial soils and is found on ridges and high flats on first bottoms of major streams. On second bottoms it grows on ridges, flats, and sloughs and can be very common in some minor stream bottoms. It develops best on clay loam ridges of new alluvium. Studies show that site quality of willow oak decreases from the higher to the lower topographic positions within a floodplain.

Willow oak is rarely found on upland sites but is occasionally seen on hardpan areas of very old terraces and on hammocks or bays. Trees on these sites are usually of poor quality.

In addition to topography, willow oak quality and growth rate are affected by soil characteristics and available moisture. In the Mississippi Delta, site quality decreases within each topographic position as clay content 30 to 46 cm (12 to 18 in) below the soil surface increases. For the non-Delta region in the South, site quality decreases within a topographic position as available potassium in the top 15 cm (6 in) of soil increases *(26)*.

The best soils for willow oak growth are those that are deep (more than 1.2 m or 4 ft), without a pan, and relatively undisturbed *(1)*. They are medium textured, silty or loamy, with no compaction in the surface for 30 cm (12 in) and are granular in the rooting zone below.

In contrast, the worst soils are shallow, have an inherent pan, or have been intensively cultivated for more than 20 years. They are fine textured, clayey, with a strongly compacted surface for 30 cm (12 in) and have a massive structure in the rooting zone.

Moisture must be readily available in the soil during the growing season for best willow oak growth. The ideal water table depth is 0.6 to 1.8 m (2 to 6 ft), while depths less than 0.3 m (1 ft) and greater than 3 m (10 ft) are unsuitable. Radial growth is not affected by standing water during the growing season (February to July) *(4)* but is greatly increased if the water table is artificially raised by impoundments to within 1.2 m (4 ft) of the soil surface *(5)*.

For best growth, the topsoil should be at least 15 cm (6 in) deep, with more than 2 percent organic matter. Optimally, soil pH in the rooting zone should be 4.5 to 5.5. The site quality worsens as the topsoil becomes more shallow, organic matter decreases, and pH departs from optimum. The soils on which willow oak is most commonly found are in the orders Inceptisols and Alfisols.

Associated Forest Cover

Willow oak is an important tree in the forest cover types Willow Oak–Water Oak–Diamondleaf Oak (Society of American Foresters Type 88) and Sweetgum–Willow Oak (Type 92). It is also a minor associate in Loblolly Pine–Hardwood (Type 82), Swamp Chestnut Oak–Cherrybark Oak (Type 91), Sugarberry–American Elm–Green Ash (Type 93), and Overcup Oak–Water Hickory (Type 96) *(22)*. Other trees associated with willow oak are water oak *(Quercus nigra)*, red maple *(Acer rubrum)*, cedar elm *(Ulmus crassifolia)*, eastern cottonwood *(Populus deltoides)*, honeylocust *(Gleditsia triacanthos)*, and persimmon *(Diospyros virginiana)*.

Swamp-privet *(Forestiera acuminata)*, roughleaf dogwood *(Cornus drummondii)*, hawthorn *(Crataegus* spp.), and American hornbeam *(Carpinus caroliniana)* are major shrub or small tree associates.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Willow oak is monoecious; male and female flowers are in separate catkins on the same tree. Staminate flowers are in slender yellow-green hairy catkins, pistillate flowers are tiny, in few flowered clusters at junction of leaf stems. Flowering occurs from February to May, about a week before the leaf buds open.

Late freezes, after the flower and leaf buds have opened, kill the flowers and defoliate the trees. New leaves develop after the freeze, but a second crop of flowers is not produced.

Seed Production and Dissemination—Seed production starts when the tree is about 20 years old. The acorns are small, 10 to 15 mm (4 to 0.6 in) in length, about as broad as long, occurring solitary or in pairs *(28)*. They mature between August and October of the second year after flowering. The first acorns to fall usually are not mature, as indicated by failure of the cup to detach easily. Good mature acorns are heavy and have a bright color with a brown micropylar end *(3)*.

Good seed crops are produced nearly every year. Mature trees produce between 9 and 53 liters (0.25 to 1.5 bu) or about 5.2 to 31.3 kg (11.5 to 69 lb) of acorns per year. Since willow oak averages 603 seeds per liter (21.250/bu) *(27)*, the number of seeds per tree ranges from about 5,400 to 31,900. Seeds are disseminated by animals and, in areas subject to overflow, by water.

Prolonged submersion of willow oak acorns reduces their germination ability slightly, but not enough to affect the species capability to regenerate an area *(13)*.

The acorns can be stored under moist, cold conditions. For germination, acorn moisture content must not drop below 40 percent; a 50 percent moisture content is preferable. Seeds should be stored at temperatures of 2° to 4° C (35° to 40° F) for 60 to 90 days before planting.

Seedling Development—Seeds germinate the spring following seedfall. Germination is hypogeal *(27)*. The best seedbed is a moist, well-aerated soil with an inch or more of leaf litter. Early height growth is moderate; on good sites in the southern part of the range, seedlings average 1.4 m (4.5 ft) in 2 years.

Willow oak normally reproduces as a single tree or in very small groups. Reproduction occurs in small to large openings created either naturally or as a result of logging. Successful regeneration usually is the result of the presence of advance regeneration before the stand is disturbed. If willow oak regeneration does not exist on the ground before disturbance, there is little chance that successful regeneration of this species will occur. Seedlings are very intolerant of saturated soil conditions except during the dormant season, when they can tolerate complete submergence without appreciable mortality. After spring foliation, complete submergence longer than 5 to 7 days can be fatal, but seedling mortality usually does not occur unless saturation periods exceed 60 days *(10)*. During saturation periods, some secondary roots are killed and no adventitious shoots are formed, height growth essentially halts. After the saturation period ends, growth of roots and shoots resumes.

Although willow oak exhibits only medium tolerance to shade, seedlings may persist for as long as 30 years under a forest canopy. They continually die back and resprout. As a result they may become misshapen. These seedling-sprouts respond to release *(12)*.

Vegetative Reproduction—Willow oak readily sprouts from stumps of small trees. Sprouts from advance reproduction are a principal method of natural regeneration. Larger diameter stumps do not sprout readily.

Cuttings taken from young parent trees can be propagated if treated with indoleacetic acid; success decreases with increasing age of the parent tree. Untreated cuttings fail completely. Layering and budding are not effective as a means of vegetative reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield—Willow oak is medium size to large, attaining 24 to 37 m (80 to 120 ft) in height and commonly 100 cm (39.5 in) in d.b.h. On good sites it makes moderately rapid growth (fig. 2). Diameter growth is dependent upon tree size. In unmanaged stands on good sites, trees 15 to 30 cm (6 to 12 in) in d.b.h. averaged 6.6 cm (2.6 in) diameter growth in 10 years *(18)*. In the 36 to 46 cm (14 to 18 in) class, they grew 7.9 cm (3.1 in) in 10 years; in the 51 to 71 cm (20 to 28 in) class, 7.1 cm (2.8 in). Dominant crop trees in a well-stocked managed stand probably average 8.9 to 10.2 cm (3.5 to 4.0 in) in d.b.h. growth in 10 years, with a maximum of 15.2 cm (6 in) *(7,26)*.

Willow oak commonly exists as a major component in mixed bottom-land stands. In a fairly typical stand near Stoneville, MS, willow oak basal area averages 7.1 m^2/ha (31 ft^2/acre) out of a total of 21.1 m^2/ha

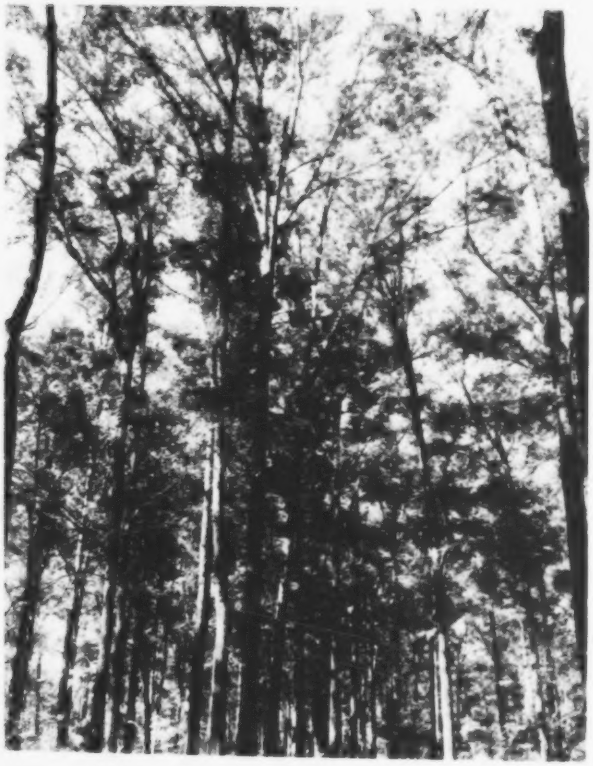

Figure 2—*A willow oak stand of excellent quality on a good site near Greenwood, MS.*

(92.0 ft²/acre) *(19)*. The same willow oak component of the stand averages 57 273 kg/ha (51,100 lb/acre) of total dry fiber, 64 percent of which is contained in the bole; 87 percent of the total is contained in trees larger than 43.2 cm (17 in).

Willow oak has been successfully planted in stream bottoms or branch heads. After 17 years, trees averaged 10.9 cm (4.3 in) in d.b.h. and 14 m (46 ft) in height *(6)*.

Rooting Habit—Where it occurs on alluvial soils, willow oak feeder roots are concentrated in the aerated layer above free water. Here they form extensive ectomycorrhizal associations that aid the tree in taking up nutrients and water and offer some protection against root diseases. Roots do not penetrate into the zone of free-standing water. In the soil region of best growth, root growth usually begins during early March.

Since complete soil saturation during the growing season inhibits root growth of seedlings, it probably has the same effect on mature trees. Production of ectomycorrhizae also is inhibited under saturated soil conditions, but once the excess soil moisture in the upper root zone dissipates, both root and mycorrhizae growth resume *(9)*. Permanent standing water, however, kills the root system and ultimately the tree.

Reaction to Competition—A straight, tall, slender trunk is common. Not a rapid pruner on good sites, it is a very ineffective natural pruner on poor sites.

A tendency exists for the production of epicormic branches if the dormant buds along the main stem are stimulated to grow by some disturbance. Among the causal disturbances are breakage of the tree crown, wounding of the stem, drought, flooding, suppression, and unsuitable sites *(16)*. Release stimulates epicormic branching on intermediate or suppressed trees, but dominant or codominant trees are much less susceptible. Thinning should aim at releasing undamaged trees pole size and larger that occupy dominant and codominant positions.

Although slow to heal from artificial pruning, live-branch wounds initially heal more rapidly than dead-branch wounds, but up to 4 years are required for healing more than 96 percent of either kind of wound *(11)*.

Willow oak is a subclimax species and is classed as intolerant of shade. All trees, except those of poor vigor, respond well to release.

Damaging Agents—Squirrels, birds, and insects (mainly acorn weevils) reduce the fruit crop, as do hogs.

A principal enemy of willow oak is fire. Seedlings and saplings are killed by even a light burn; hot fires kill larger trees. Trees not immediately killed by the fire are often wounded and become susceptible to butt rot fungi.

A common canker on bottom-land willow oaks is caused by *Polyporus hispidus (25)*. This insidious fungus grows rapidly, cankers lengthening 10 to 15 cm (4 to 6 in) per year, and may cause as much as 25 percent cull in some areas. Cankered trees should be removed as soon as possible, both to salvage the log and to remove the tree as a source of infection *(15)*.

Perhaps the most serious insect pests are the trunk borers. They cause serious degrade in saw log quality. Three of the more common are the red oak borer *(Enaphalodes rufulus)*, carpenterworm *(Prionoxystus robiniae)*, and living-beech borer *(Goes pulverulentus) (23,24)*.

Willow oak has been shown to be susceptible to acid rain, the foliage showing yellow or brown necrotic zones when exposed to simulated rain of less than 3.2 pH *(20)*.

Special Uses

Since it produces an acorn crop almost every year, willow oak is an important species for wildlife food production. In addition to being a major supplier of food for game animals such as ducks, squirrels, deer, and turkey, willow oak supplies many other animals. Blue jays and red-headed woodpeckers are major consumers, while grackles, flickers, mice, and flying squirrels utilize the tree itself *(8)*.

A favored shade tree, it is widely planted as an ornamental. It is also a good species to plant along margins of fluctuating-level reservoirs *(21)*. Willow oak can be harvested when quite young and utilized as biomass *(17)*. Pulp yields per unit volume of young versus old trees do not differ greatly and chemical demand in pulping is not greatly increased *(2)*.

Willow oak is being utilized in hardwood plantations, since it gives a good combination of pulping characteristics and growth rate.

Genetics

No racial variations of willow oak are known, but the following hybrids are recognized *(14)*: *Quercus phellos* × *nigra* (*Q.* × *capesii* W. Wolf); *Q. phellos* × *velutina* (*Q.* × *filialis* Little); *Q. phellos* × *ilicifolia* (*Q.* × *giffordii* Trel.); *Q. phellos* × *rubra* (*Q. heterophylla* Michx. f.); *Q. phellos* × *falcata* (*Q.* × *ludoviciana* Sarg.); *Q. phellos* × *shumardii* (*Q.* × *moultonensis* Ashe); *Q. phellos* × *marilandica* (*Q. rudkinii* Britton); *Q. phellos* × *palustris* (*Q.* × *schociana* Dieck.).

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Quercus prinus L. Chestnut Oak

Fagaceae Beech family

Robert A. McQuilkin

Chestnut oak *(Quercus prinus)*, sometimes called rock chestnut oak, rock oak, or tanbark oak, is commonly found in the Appalachian region on dry, infertile soils and rocky ridges but reaches best growth on rich well-drained soils along streams. Good acorn crops on this medium-sized, long-lived tree are infrequent, but the sweet nuts are eaten by wildlife when available. Chestnut oak is slow growing and the lumber is cut and sold as white oak.

Habitat

Native Range

Chestnut oak (figs. 1, 2) extends from southwestern Maine west through New York to extreme southern Ontario, southeastern Michigan, southern Indiana and Illinois, south to northeastern Mississippi, and east to central Alabama and Georgia; then north to Delaware, mostly west of the Coastal Plain. Its best growth occurs in the mountains of the Carolinas and Tennessee *(18)*.

Climate

The climate throughout most of the range of chestnut oak is humid, with small superhumid areas in the Appalachian Mountains. The average annual precipitation varies from 810 mm (32 in) in western New York and southern Ontario to more than 2030 mm (80 in) in the southern Appalachians; however, annual precipitation for the majority of the chestnut oak range is between 1020 and 1220 mm (40 and 48 in). Length of growing season varies from 120 days in New England to 240 days in northern Alabama and Georgia *(18)*.

Soils and Topography

Chestnut oak is most commonly found on dry upland sites such as ridgetops and upper slopes with shallow soils, south- and west-facing upper slopes, and sandy or rocky soils with low moisture-holding capacity of the orders Ultisols and Inceptiols. Chestnut oak grows from near sea level on the Coastal Plain of New Jersey and Long Island to elevations of approximately 1400 m (4,600 ft) in the southern Appalachians *(4,8)*.

In the Blue Ridge Mountains of northern Georgia, site index for chestnut oak ranges from 12 to 25 m (39 to 83 ft), and averages about 20 m (65 ft). Site index is greater on steep slopes, lower slope positions, and at elevations below 800 m (2,600 ft) than elsewhere. Other indicators of good chestnut oak sites are subsoils with more than 15 percent silt, loam or sandy loam surface soils, and sites where litter decomposes rapidly *(15)*. Chestnut oak growth is poorest on soils of the Porters (Humic Hapludult) and Ashe (Typic Dystrochrept) series, intermediate on soils of the Hayesville and Halewood series (Typic Hapludults), and best on soils of the Tusquitee and Brevard series (Humic and Typic Hapludults, respectively) *(6)*.

Associated Forest Cover

Chestnut oak is a major component in 2 forest cover types and an associated species in 10 others *(8)*. Chestnut Oak (Society of American Foresters Type 44) is found primarily on dry south- and west-facing slopes, ridgetops, and rocky outcrops throughout the Appalachian Mountains at elevations from 450 to 1400 m (1,475 to 4,600 ft). Associated species in this type vary greatly by region, elevation, topographic position, and soils, and include other upland oaks *(Quercus* spp.) and hickories *(Carya* spp.); sweet birch *(Betula lenta)*; yellow-poplar *(Liriodendron tulipifera)*; blackgum *(Nyssa sylvatica)*; sweetgum *(Liquidambar styraciflua)*; black cherry *(Prunus serotina)*; black walnut *(Juglans nigra)*; red *(Acer rubrum)* and sugar *(A. saccharum)* maples; eastern redcedar *(Juniperus virginiana)*; eastern hemlock *(Tsuga canadensis)*; and red *(Pinus resinosa)*, eastern white *(P. strobus)*, pitch *(P. rigida)*, Table Mountain *(P. pungens)*, shortleaf *(P. echinata)*, Virginia *(P. virginiana)*, and longleaf *(P. palustris)* pines. A variant of this type, chestnut oak–northern red oak, is found in disturbed forests in the Catskills in New York and on Massanutten Mountain in Virginia. The variant chestnut oak–scarlet oak is identified in the central Appalachians, while the variants chestnut oak–pitch pine, chestnut oak–eastern white pine–northern red oak, and chestnut oak–black oak–scarlet oak occur in the southern Appalachians.

White Pine–Chestnut Oak (Type 51) is found in the Appalachian region from West Virginia to Georgia. It is most common in southwestern Virginia, eastern

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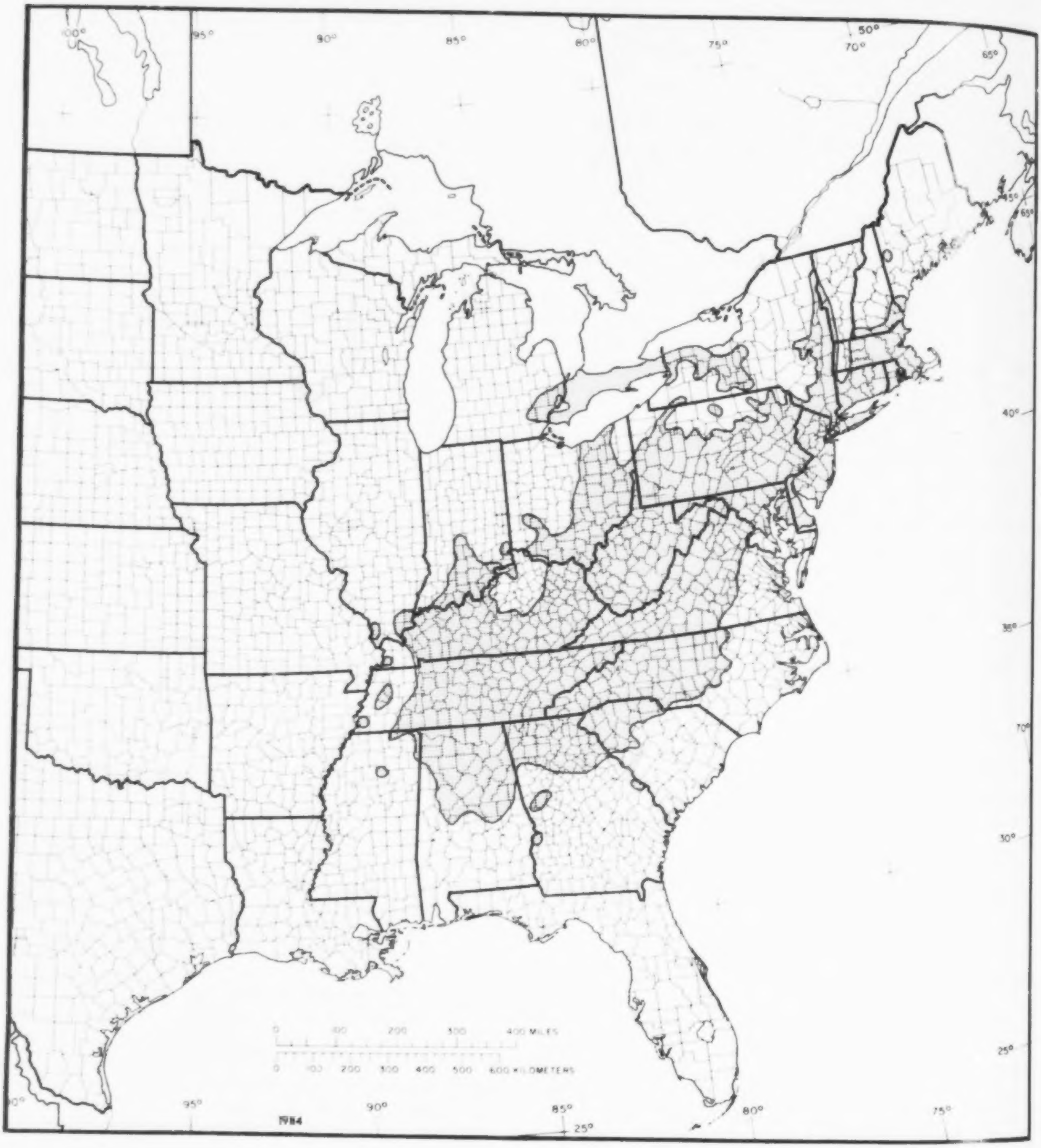
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Figure 1—*The native range of chestnut oak.*

Figure 2—*Chestnut oak.*

Tennessee, and western North Carolina at elevations between 360 and 1100 m (1,200 and 3,600 ft). On the drier sites, common associated species include scarlet *(Quercus coccinea)*, white *(Q. alba)*, post *(Q. stellata)*, and black *(Q. velutina)* oaks; hickories; blackgum; sourwood *(Oxydendrum arboreum)*; red maple; and pitch, Table Mountain, Virginia, and shortleaf pines. On more mesic sites, associated species include northern red *(Quercus rubra)* and white oaks, black locust *(Robinia pseudoacacia)*, yellow-poplar, sugar and red maples, and black cherry.

Chestnut oak is also an associated species in the following cover types: Eastern White Pine (Type 21); White Pine–Hemlock (Type 22); Red Maple (Type 108); Bear Oak (Type 43); White Oak–Black Oak–Northern Red Oak (Type 52) and its variants white oak–black oak–chestnut oak, black oak–scarlet oak–chestnut oak, and scarlet oak–chestnut oak; White Oak (Type 53); Black Oak (Type 110); Pitch Pine (Type 45) and its variant pitch pine–chestnut oak; Virginia Pine (Type 79); and Virginia Pine–Oak (Type 78).

Common shrub associates of chestnut oak include highbush and lowbush blueberry *(Vaccinium corymbosum* and *V. angustifolium)*, dwarf chinkapin oak *(Quercus prinoides)*, and mountain-laurel *(Kalmia latifolia)*.

Before the demise of American chestnut *(Castanea dentata)*, chestnut oak was an important component of the Appalachian oak–chestnut forests. Since then, hickory, chestnut oak, northern red oak, and white oak have replaced American chestnut as these stands have gradually changed to oak-hickory stands *(20)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Chestnut oak is monoecious; the flowers develop in the spring at the time of bud-break and leaf development. The staminate flowers are borne on aments (catkins) that originate from buds in the terminal bud cluster of the previous year's shoots. Development of the aments begins with the first expansion of these buds, when minimum air temperatures remain above 10° C (50° F) for more than 10 days. Pistillate flowers develop on short stalks in the axils of the new leaves from 5 to 10 days after the aments emerge. Pollination is by wind; pollen dispersal occurs 10 to 20 days after the aments emerge and is controlled largely by weather. Above-normal temperatures in late April followed by 13 to 20 days of below-normal temperatures in early May enhance successful pollination and the development of large acorn crops. The early warm period promotes the development of the aments, shoot expansion, and pistillate flower development, and the later cool period delays pollen dispersal to better coincide with pistillate flower maturation. Uniformly increasing temperatures during this period usually result in poor pollination and small acorn crops *(27,28)*.

Chestnut oak produces an abundant crop of aments every year, but the production of pistillate flowers varies considerably from year to year; trees that produce a large crop of flowers and acorns one year usually produce fewer flowers the following year.

Seed Production and Dissemination—Chestnut oak acorns mature in one growing season and drop from early September to early October, 2 to 5 weeks before the acorns of other upland oaks. Production of chestnut oak acorns is erratic, and heavy crops occur only once every 4 or 5 years. In general, chestnut oak produces fewer acorns than other upland oaks, although occasional trees can be prolific seed producers *(2)*.

Chestnut oak begins producing seed at about age 20, but stump sprouts as young as 3 years can produce viable seed, and coppice stands as young as 7 or 8 years can have abundant acorn production. The germinative capacity of sound acorns is around 90 percent. Dissemination is primarily by gravity and squirrels *(4,22,26)*.

Seedling Development—Chestnut oak acorns have no dormancy and therefore germinate in the fall. Germination is hypogeal *(22)*. If temperatures are below 16° C (61° F), however, shoot (but not root) development is inhibited by an induced epicotyl dormancy. This dormancy is broken by chilling during the winter, and normal shoot development resumes in the spring *(9)*. Some acorns germinate at day/night temperatures of 10°/2° C (50°/35° F), but most germinate at temperatures at or above 18°/10° C or 65°/50° F). Chestnut oak acorns are much more capable of germinating in dry soil than acorns of white, black, or northern red oak. This difference may be due to a thick parenchyma layer in the acorn pericarp that allows them to absorb and retain more moisture than acorns of other oaks *(17)*.

Germination of chestnut oak acorns is enhanced by a covering of leaf litter 2 or 3 cm (1 in) deep, but a covering of more than about 5 cm (2 in) results in many etiolated seedlings. Large numbers of seedlings can become established after good seed years, but such years occur infrequently. Seedling establishment and survival are greatly reduced by dense herbaceous and shrub layers.

Chestnut oak seedlings grow slowly. In Indiana, the height of seedlings 10 years after establishment averaged 15 cm (6 in) in an uncut forest, 24 cm (9 in) where release cuttings were made, and 146 cm (58 in) in a clearcut. In contrast to this slow seedling growth, chestnut oak sprouts in the clearcut were more than 6.4 m (21 ft) tall *(4)*. The seedlings are capable of rapid growth, however, when growing conditions are near optimal. In one nursery study, chestnut oak seedlings produced an average of 4.3 growth flushes during the first growing season and exceeded bear oak and white oak, and equaled or exceeded northern red oak in height, dry weight, and leaf area. Growth of these seedlings was highly correlated with initial leaf area, which in turn was correlated with acorn size *(11)*.

Vegetative Reproduction—When tops die back or are damaged, chestnut oak seedlings and advance reproduction sprout vigorously from dormant buds at the root collar or on the stem. For stems of advanced reproduction that have been cut, the number of sprouts per plant and the growth of the sprouts increase with increasing size of the original stem and root system *(25)*. Stumps of cut trees up to 60 years of age sprout vigorously, but the percent of stumps that sprout declines with increasing size for trees more than 46 cm (18 in) in d.b.h. Incidence of decay is low for stump sprouts that originate within 5 cm (2 in) of the ground and such sprouts can develop into high-quality trees. Sprouting frequency and vigor are greater from stumps of trees cut during the dormant season than from those cut during the growing season *(24,35)*.

It has been estimated that 75 percent of the chestnut oak reproduction in the southern Appalachians is of sprout origin *(4)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Chestnut oak is a medium-size tree; at maturity it usually attains a height of 20 to 24 m (65 to 80 ft) and a d.b.h. of 51 to 76 cm (20 to 30 in) depending on site quality. Maximum dimensions are approximately 30 m (100 ft) in height and 183 cm (72 in) in d.b.h. *(4)*. In mixed oak stands, the height growth of adjacent dominant and codominant chestnut, scarlet, northern red, and black oaks is about equal and is greater than that of white oaks *(7,33)*. White, chestnut, black, and scarlet oaks of equal site index (height at base age 50 years) have similar height growth patterns up to about age 60. Beyond this age, white oak maintains a better height growth rate than the other three species and, at site indexes below about 18.3 m (60 ft) chestnut oak maintains a height growth intermediate between that of white oak and the black and scarlet oaks *(5)*. On comparable sites in West Virginia, diameter growth of chestnut oak is generally greater than that of white oak, the same as that of scarlet oak, hickory, and beech *(Fagus grandifolia)*, but less than that of northern red and black oaks, yellow-poplar, sugar maple, basswood *(Tilia americana)*, black cherry, and white ash *(Fraxinus americana)* *(30,31)*.

Sawtimber yield from chestnut oak stands on dry slopes and ridges in the southern Appalachians is about 98.0 m^3/ha (7,000 fbm/acre) at age 80. On average sites, maximum periodic growth is about 1.4 m^3/ha (100 fbm/acre) per year at age 100 *(4)*.

On the better sites, chestnut oak has good form and maintains a bole that is relatively clear of branches and sprouts, although many epicormic sprouts develop if the bole is exposed to sunlight *(32)*.

Rooting Habit—Chestnut oak seedlings initially develop a deep tap root but later lose this configuration. Saplings and larger trees have a root system consisting of 6 to 10 main lateral roots extending 3 to 10 m (10 to 33 ft) from the root crown at depths from near the soil surface to 91 cm (36 in). Numerous secondary roots branch off these main laterals, and a dense mat of fine roots develops near the soil surface. The root system extends over an area approximately five times that of the crown area. The roots of chestnut oak are slightly deeper than those of northern red oak but not as deep as those of white oak *(29)*.

Chestnut oak seedlings maintain much higher root starch levels during the growing season than white oak or northern red oak and have a higher root-to-shoot ratio and a more rapid initial root development rate than northern red oak. These factors may partially account for the species adaptability to xeric sites *(10,16)*.

Reaction to Competition—Chestnut oak is intermediate in shade tolerance. Among the oaks, it is similar in tolerance to white oak, but more tolerant than northern red, black, or scarlet oak. In closed stands in the Appalachian region, most chestnut oak reproduction lives only a few years. In partial shade, however, seedling sprout advance reproduction may persist for many years. These stems grow slowly and die back and resprout periodically but are capable of rapid growth if released.

In the Appalachian region, chestnut oak typically occupies intermediate to poor sites where it is considered to be the physiographic climax. It is excluded from the more mesic sites by species that grow more rapidly in the seedling and sapling stages, such as northern red, black, and white oaks; yellow-poplar; sugar and red maples; and black cherry. The most xeric sites are typically occupied by species even better adapted to such conditions, such as scarlet oak, post oak, and pitch pine *(8,21,23)*.

Damaging Agents—Because of its predominance on steep slopes and dry sites, chestnut oak has a higher incidence of fire damage and associated decay than other oaks throughout the Appalachians, although its inherent resistance to heartwood decay is greater than that of white, northern red, black, or scarlet oak. Chestnut oak is susceptible to most of the diseases of oaks including oak wilt (*Ceratocystis fagacearum*). It is particularly susceptible to the twig-blight fungus *Diplodia longispora*, a die-back and branch canker caused by *Botryodiplodia* spp., and, from Virginia northward, stem cankers caused by *Nectria galligena* and *Strumella coryneoidea*. The heartrot fungi *Spongipellis pachyodon* commonly occurs around dead branch stubs on chestnut oak in the southeast. Sprout rot, caused primarily by the heart rot fungi *Stereum gausapatum*, *Fistulina hepatica*, and *Armillaria mellea*, is common in chestnut oak stump sprouts that originate 5 cm (2 in) or more above the ground line, although the incidence of this rot is less in chestnut oak than in other oaks. The more important decay-causing fungi of chestnut oak in Ohio, Kentucky, Indiana, and Illinois are *Inonotus andersonii*, *Stereum gausapatum*, *Spongipellis pachyodon*, *Wolfiporia cocos*, *Inonotus dryophilus*, *Xylobolus frustulatus*, *Perenniporia compacta*, and *Armillaria mellea (3,13)*.

Chestnut oak and white oak are the two species most preferred by the gypsy moth (*Lymantria dispar*). Other important defoliators of chestnut oak are the spring and fall cankerworms (*Paleacrita vernata* and *Alsophila pometaria*), the forest tent caterpillar (*Malacosoma disstria*) and the half-wing geometer (*Phigalia titea*) *(1,14,34)*.

Chestnut oak is more resistant to wood borers than most oaks but is particularly susceptible to attack by ambrosia beetles, especially the Columbian timber beetle (*Corthylus columbianus*) and several species of the genera *Platypus* and *Xyleborus*; these beetles are particularly damaging to trees that have been weakened by fire or drought. The more important wood borers that attack chestnut oak are the oak timberworm (*Arrhenodes minutus*), the carpenterworm (*Prionoxystus robiniae*), and the little carpenterworm (*P. macmurtrei*).

Chestnut oaks are also susceptible to several gall-forming wasps (*Cynipidae*), a pit scale (*Asterolecanium quercicola*), and the golden oak scale (*A. variolosum*). These insects may kill twigs and branches but rarely kill mature trees.

The acorns of chestnut oak are frequently infested with larvae of the nut weevils *Curculio* spp. and *Conotrachelus* spp., the moth *Valentinia glandulella*, and the cynipid gall wasps (*Cynipidae*). However, one study indicated that chestnut oak acorns may have lower insect infestation rates than acorns of other oaks *(2)*.

Special Uses

The acorns of chestnut oak, along with those of the other oaks, are an important food for many wildlife species including deer, turkeys, squirrels, chipmunks, and mice. Chestnut oak lumber is similar to and marketed as white oak *(12)*.

Genetics

No races of chestnut oak are known. Chestnut oak hybridizes with *Quercus alba* (*Q.* × *saulii* Schneid.);

Q. bicolor; Q. robur (Q. × *sargentii* Rehd.); and *Q. stellata (Q.* × *bernardiensis* W. Wolf) *(19).*

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Quercus rubra L. Northern Red Oak

Fagaceae Beech family

Ivan L. Sander

Northern red oak *(Quercus rubra)*, also known as common red oak, eastern red oak, mountain red oak, and gray oak, is widespread in the East and grows on a variety of soils and topography, often forming pure stands. Moderate to fast growing, this tree is one of the more important lumber species of red oak and is an easily transplanted, popular shade tree with good form and dense foliage.

Habitat

Native Range

Northern red oak (fig. 1) is the only native oak extending northeast to Nova Scotia. It grows from Cape Breton Island, Nova Scotia, Prince Edward Island, New Brunswick, and the Gaspé Peninsula of Quebec, to Ontario, in Canada; from Minnesota south to eastern Nebraska and Oklahoma; east to Arkansas, southern Alabama, Georgia, and North Carolina. Outliers are found in Louisiana and Mississippi *(17)*.

Climate

In the wide area over which northern red oak grows, mean annual precipitation varies from about 760 mm (30 in) in the Northwest to about 2030 mm (80 in) in the southern Appalachians. Annual snowfall ranges from a trace in southern Alabama to 254 cm (100 in) or more in the Northern States and Canada. Mean annual temperature is about 4° C (40° F) in the northern part of the range and 16° C (60° F) in the extreme southern part. The frost-free period averages 100 days in the North and 220 days in the South *(24)*.

Soils and Topography

In the north, northern red oak grows on cool moist Boralfs and Orthod Spodosols. Elsewhere it grows on warm moist soils including Udalf Alfisols, Dystrochrept and Fragiochrept Inceptisols, Udoll Mollisols, Rhodic Paleudult, Humic and Mesic Hapludult Udult Ultisols, and small areas of Udipsamment Entisols. The most widespread soils are the Udalfs and Udolls *(33)*.

These soils are derived from glacial material, residual sandstones, shale, limestone, gneisses, schists, and granites. They vary from clay to loamy sands and some have a high content of rock fragments. Northern red oak grows best on deep, well-drained loam to silty, clay loam soils *(24)*.

Although northern red oak (fig. 2) is found in all topographic positions, it always grows best on lower and middle slopes with northerly or easterly aspects, in coves and deep ravines, and on well-drained valley floors. It grows at elevations up to 1070 m (3,500 ft) in West Virginia and up to 1680 m (5,500 ft) in the southern Appalachians *(24)*.

The most important factors determining site quality for northern red oak are depth and texture of the A soil horizon, aspect, and slope position and shape. The best sites are found on lower, concave slopes with a northerly or easterly aspect, on soils with a thick A horizon, and a loam to silt loam texture. Other factors may affect site quality in localized areas such as depth to water table in southern Michigan and annual precipitation up to 1120 mm (44 in) in northwestern West Virginia *(2,24)*.

Associated Forest Cover

Northern Red Oak (Society of American Foresters Type 55) is the forest cover type that includes pure stands of this tree or stands in which it is predominant *(6)*. The species is a major component of White Pine–Northern Red Oak–Red Maple (Type 20) in the Northern Forest Region, and it is a principal species in White Oak–Black Oak–Northern Red Oak (Type 52) in the Central Forest Region. Northern red oak is listed as an associated species in the following forest types:

17	Pin Cherry
18	Paper Birch
19	Gray Birch–Red Maple
21	Eastern White Pine
22	White Pine–Hemlock
23	Eastern Hemlock
25	Sugar Maple–Beech–Yellow Birch
26	Sugar Maple–Basswood
27	Sugar Maple
28	Black Cherry–Maple
40	Post Oak–Blackjack Oak
42	Bur Oak
43	Bear Oak
44	Chestnut Oak
45	Pitch Pine

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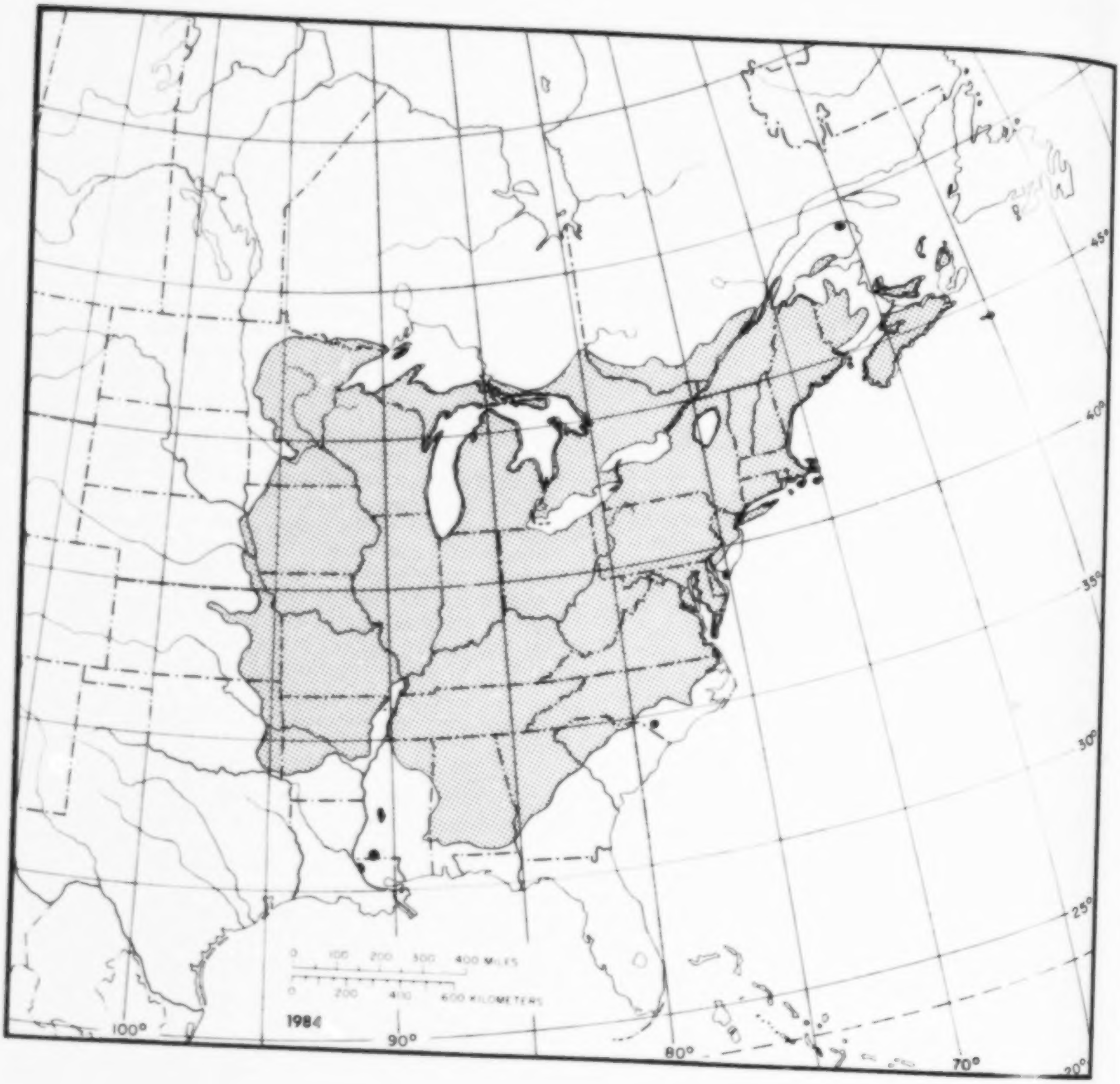
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Figure 1—*The native range of northern red oak.*

46	Eastern Redcedar
51	White Pine–Chestnut Oak
53	White Oak
57	Yellow-Poplar
58	Yellow-Poplar–Eastern Hemlock
60	Beech–Sugar Maple
82	Loblolly Pine–Hardwood
108	Red Maple
110	Black Oak

Numerous other tree species are associated with northern red oak. These include white ash (*Fraxinus americana*) and green ash (*F. pennsylvanica*); bigtooth aspen (*Populus grandidentata*) and quaking

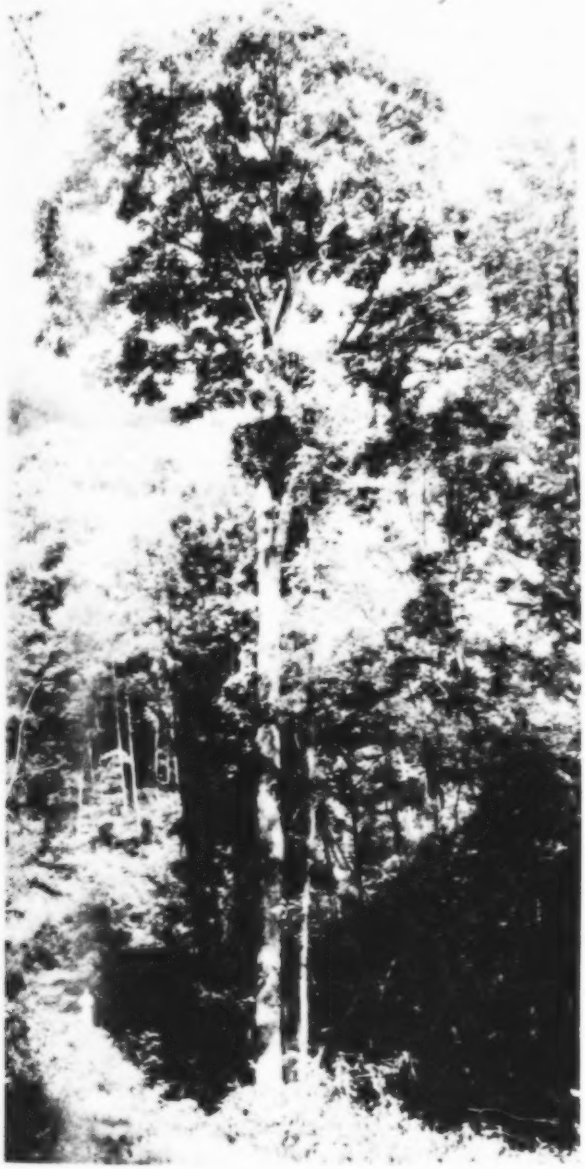

Figure 2—*A mature northern red oak growing in the southern Appalachians at an elevation of 945 m (3,100 ft). The tree is 90 cm (35 in) in d.b.h. and 46 m (151 ft) tall.*

aspen (*P. tremuloides*); American elm (*Ulmus americana*) and slippery elm (*U. rubra*); pignut hickory (*Carya glabra*), bitternut hickory (*C. cordiformis*), mockernut hickory (*C. tomentosa*), and shagbark hickory (*C. ovata*); scarlet oak (*Quercus coccinea*), southern red oak (*Q. falcata*), post oak (*Q. stellata*), and chinkapin oak (*Q. muehlenbergii*); northern white-cedar (*Thuja occidentalis*); yellow buckeye (*Aesculus octandra*); cucumber magnolia (*Magnolia acuminata*); hackberry (*Celtis occidentalis*); butternut (*Juglans cinerea*); black walnut (*J. nigra*); blackgum (*Nyssa sylvatica*); and sweetgum (*Liquidambar styraciflua*) (*5*).

Some of the more important small trees associated with northern red oak include flowering dogwood (*Cornus florida*), sourwood (*Oxydendrum arboreum*), American holly (*Ilex opaca*), eastern hophornbeam (*Ostrya virginiana*), American hornbeam (*Carpinus caroliniana*), redbud (*Cercis canadensis*), pawpaw (*Asimina triloba*), sassafras (*Sassafras albidum*), persimmon (*Diospyros virginiana*), American bladdernut (*Staphylea trifolia*), and downy serviceberry (*Amelanchier arborea*). Shrubs common in forest stands containing northern red oak include *Vaccinium* spp., mountain-laurel (*Kalmia latifolia*), rosebay rhododendron (*Rhododendron maximum*), witch-hazel (*Hamamelis virginiana*), beaked hazel (*Corylus cornuta*), spice bush (*Lindera benzoin*), and *Viburnum* spp. The most common vines are Virginia creeper (*Parthenocissus quinquefolia*), poison-ivy (*Toxicodendron radicans*), greenbrier (*Smilax* spp.), and grape (*Vitis* spp.) (*5*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Northern red oak is monoecious. The staminate flowers are borne in catkins that develop from leaf axils of the previous year and emerge before or at the same time as the current leaves in April or May. The pistillate flowers are solitary or occur in two- to many-flowered spikes that develop in the axils of the current year's leaves. The fruit is an acorn or nut that occurs singly or in clusters of from two to five, is partially enclosed by a scaly cup, and matures in 2 years. Northern red oak acorns are brown when mature and ripen from late August to late October, depending on geographic location (*30*).

Seed Production and Dissemination—In forest stands northern red oak begins to bear fruit at about age 25 but usually does not produce seeds abundantly until about age 50. Good to excellent seed crops are produced at irregular intervals, usually every 2 to 5 years (*30*).

Acorn production is highly variable among trees even in good seed years. Some trees are always poor producers while others are always good producers.

Crown size seems to be the most important tree characteristic affecting acorn production. Dominant or codominant trees with large, uncrowded crowns produce more acorns than trees with small, restricted crowns *(24)*.

Even in good years only about 1 percent of the acorns become available for regeneration in northern red oak, and as many as 500 or more acorns may be required to produce one 1-year-old seedling. Many acorns are consumed by insects, squirrels, small rodents, deer, and turkey and other birds. They can eat or damage more than 80 percent of the acorn crop in most years and virtually 100 percent of the crop in very poor seed years *(19,24,28)*. The large acorns are generally dispersed over only short distances. Gravity and the caching activities of squirrels and mice are the primary means of dispersal.

Seedling Development—Northern red oak seedlings that are established naturally or by planting at the time an old stand is clearcut, regardless of how large the clearcut area, do not grow fast enough to compete with the vigorous woody sprouts and other vegetation *(4,29)*. The species will be present in new reproduction stands in proportion to the amount of advance reproduction present before complete overstory removal. To compete successfully in new stands, stems of northern red oak advance reproduction must be large and have well-established root systems. Thus, achieving successful northern red oak reproduction depends on creating conditions necessary for establishing seedlings and for their survival and growth *(27,29)*.

Northern red oak acorn germination is hypogeal *(30)*. It occurs during the spring following seedfall. Best germination occurs when the acorns are in contact with or buried in mineral soil and covered by a thin layer of leaf litter. Acorns on top of the leaf litter or mixed with litter generally dry excessively during early spring and lose their viability before temperatures are favorable for germination *(24,28)*.

Although available soil moisture can be a critical factor affecting first year survival of northern red oak seedlings, it is usually adequate at the time acorns germinate. Germination is followed by vigorous and rapid taproot development, and if the taproot is able to penetrate the soil, seedlings survive considerable moisture stress later in the growing season. Northern red oak seedlings are less drought tolerant than white or black oak seedlings, however *(24,31)*.

Light intensity appears to be the most critical factor affecting not only first year survival, but also survival and growth in subsequent years *(20,28)*. Northern red oak reaches maximum photosynthesis at about 30 percent of the light intensity in the open *(21)*. Light intensity under forest stands is often much lower, however, at about 15 cm (6 in) above the ground, where the new seedlings are competing. Light intensity at this level under forest stands in Missouri has been documented to be 10 percent or less of that in the open, a level too low to allow seedlings to survive and grow.

Once established under a forest stand, northern red oak seedlings seldom remain true seedlings for more than a few years. Conditions such as fire, poor light, poor moisture conditions, or animal activity kill the tops, but not the roots. One or more dormant buds near the root collar then produce new sprouts. This dieback and resprouting may occur several times; the result is a crooked, flat-topped, or forked stem. Such stems have root systems that may be from 10 to 15 years or more older than the tops *(29)*.

Northern red oak shoot growth is episodic. When moisture, light, and temperature conditions are favorable, multiple shoot growth flushes will occur in the same growing season. The first flush is generally the longest and each flush is followed by a distinctive rest period. Most of the annual root elongation occurs during the rest periods *(22)*.

Growth of northern red oak advance reproduction, seedlings, and sprouts is slow and generally restricted to one growth flush under undisturbed or lightly disturbed forest stands; at best it averages only a few centimeters annually *(28)*.

Vegetative Reproduction—Northern red oak sprouts readily. More than 95 percent of the northern red oaks in new production stands are sprouts, either from advance reproduction or from stumps of cut trees. New sprouts from advance reproduction arise when old stems are damaged during logging. Height growth of new sprouts is related to the size of the old, damaged stem; the larger the old stem, the faster the new sprout will grow *(25,26)*. New sprouts grow rapidly and are usually straight and well formed.

Northern red oak stumps sprout more frequently than black oak or white oak stumps but about the same as scarlet and chestnut oak stumps *(27)*. Sprouting frequency is related to parent tree size with more small stumps sprouting than large ones. Large stumps tend to produce more sprouts than small ones but by about age 20 to 25 the number of living sprouts per stump averages four or five regardless of parent tree or stump size. Northern red oak stump sprouts grow rapidly, averaging about 61 cm (24 in) or more annually for about 30 years *(14)*. These stump sprouts can be a valuable component of new reproduction stands particularly if they originate at or near the ground line. Sprouts of low origin are much less likely to develop decay than sprouts that originate high on the stump *(24)*, but they tend to develop severe crook or sweep at the base. Early clump thinning may be desirable to improve potential quality although it is not needed to maintain good growth.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature northern red oaks are usually from 20 to 30 m (65 to 98 ft) tall and 61 to 91 cm (24 to 36 in) in d.b.h. in undisturbed stands on good sites. Forest-grown trees develop a tall, straight columnar bole and large crowns. Open-grown trees tend to have short boles and spreading crowns *(24)*.

Average diameter growth of northern red oak for a range of ages, sites, and stand conditions in the Central States is about 5 mm (0.2 in) annually *(9)*. On good sites in the Appalachians, dominant and codominant northern red oaks in even-aged stands may attain average annual diameter growth rates of about 10 cm (0.4 in) and on average sites about 6 mm (0.25 in) by age 50 or 60 *(32)*.

Growing space requirements are not known for northern red oak in pure stands, but average requirements have been developed for mixed oaks in even-aged stands. Competition for growing space begins when the available space in a stand is equal to the total of the maximum requirements of all the trees in the stand. This is the lowest level of stocking for full site utilization and is about 60 percent of full stocking. The minimum growing space for a tree 15.2 cm (6 in) in d.b.h. to survive averages about 8.5 m^2 (92 ft^2). If that tree is in the open or completely free from competition, the maximum amount of growing space it can use is 14.4 m^2 (155 ft^2). For a tree 53.3 cm (21 in) in d.b.h., minimum and maximum growing spaces are 26.5 m^2 (285 ft^2) and 45.7 m^2 (492 ft^2), respectively. Experience in using the stocking standards developed by Gingrich *(8)* indicates that a northern red oak tree requires less growing space than trees of other oak species with the same diameter *(10,18)*. How much less growing space is required has not been determined, however.

Yields of unthinned, 80-year-old oak stands in the Central States that contain northern red oak range from 75.6 m^3/ha (5,400 fbm/acre) on site index 16.8 m (55 ft) sites (base age 50 years) to 175.0 m^3/ha (12,500 fbm/acre) on site index 22.9 m (75 ft) sites. At age 70, oak stands that are first thinned at age 20 and then thinned regularly to the lowest level of stocking for full site utilization at about 10-year intervals will yield about 102.9 m^3/ha (7,350 fbm/acre) on site index 16.8 m (55 ft) sites and about 278.3 m^3/ha (19,880 fbm/acre) on site index 22.9 m (75 ft) sites *(9)*. In southern Michigan, the average yields of 80-year-old unmanaged stands containing northern red oak ranged from 12.6 m^3/ha (900 fbm/acre) to 3.5 m^3/ha (250 fbm/acre) on poor sites and from 154.0 m^3/ha (11,000 fbm/acre) to 280.0 m^3/ha (20,000 fbm/acre) on good sites *(1)*.

Rooting Habit—No information available.

Reaction to Competition—Northern red oak is classed as intermediate in shade tolerance. It is less tolerant than some of its associates such as sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), basswood (*Tilia americana*), and the hickories but more tolerant than others such as yellow-poplar (*Liriodendron tulipifera*), white ash, and black cherry (*Prunus serotina*). Among the oaks, it is less shade tolerant than white and chestnut and about equal with black and scarlet *(24)*.

Northern red oak responds well to release if the released trees are in the codominant or above average intermediate crown classes *(11)*. The best response to thinning or release is obtained if the thinning or release is made before an even-aged stand containing northern red oak is 30 years old. Trees in well-stocked stands 30 years old and older generally have small, restricted crowns and are unable to make efficient use of the growing space provided by thinning or release *(24)*. In Arkansas, 50-year-old released crop trees averaged a 40-percent increase in diameter growth over unreleased trees in the 10 years immediately following release. Although diameter growth increased the first year after release, the greatest responses ocurred in years 5-10 when growth of the released trees averaged about 0.5 cm (0.2 in) annually and was about twice that of unreleased trees *(11)*. Epicormic branching can be prolific on northern red oak following heavy thinning in stands older than about 30 years. Trees around the perimeter of openings created by harvesting may also develop many epicormic branches, because the boles of northern red oak in fully stocked stands contain numerous dormant buds. When the boles are suddenly exposed to greatly increased light, these buds begin to grow *(27)*.

Damaging Agents—Wildfires seriously damage northern red oak by killing the cambial tissue at the base of trees, thus creating an entry point for decay-causing fungi. Wildfires can be severe enough to top kill even pole- and sawtimber-size trees. Many of the top-killed trees sprout and thus create new even-aged stands, but the economic loss of the old stand may be great *(24)*. Small northern red oak seedlings may be killed by prescribed fires *(13)*, but larger stems will sprout and survive, even if their tops are killed.

Oak wilt *(Ceratocystis fagacearum)* is a potentially serious vascular disease of northern red oak and kills trees the same year they are infected. It usually kills individuals or small groups of trees in scattered locations throughout a stand but may affect areas up to several hectares in size. Oak wilt is spread from tree to tree through root grafts and over longer distances by sap-feeding beetles *(Nitidulidae)* and the small oak bark beetles *(Pseudopityophthorus* spp.) *(12,23)*.

Shoestring root rot *(Armillaria mellea)* attacks and may kill northern red oaks that have been injured or weakened by fire, lightning, drought, insects, or other diseases. Cankers caused by *Strumella* and *Nectria* species damage the bole of northern red oak and although trees are seldom killed, the infected trees are generally culls for lumber. Foliage diseases that attack northern red oak but seldom do serious damage are anthracnose *(Gnomonia quercina)*, leaf blister *(Taphrina* spp.), powdery mildews *(Phyllactinia corylea* and *Microsphaera alni)*, and eastern gall rust *(Cronartium quercuum) (12)*.

The carpenterworm *(Prionoxystus robiniae)*, Columbian timber beetle *(Corythylus columbianus)*, oak timberworm *(Arrhenodes minutus)*, red oak borer *(Enaphalodes rufulus)*, and the twolined chestnut borer *(Agrilus bilineatus)* are important insects that attack the bole of northern red oak. These insects tunnel into the wood, seriously degrading products cut from infested trees *(3)*.

The most destructive defoliating insect attacking northern red oak is the imported gypsy moth *(Lymantria dispar)*. This insect repeatedly defoliates trees and has killed oaks including northern red oak in a wide area in the northeastern United States. Northern red oak can recover from a single defoliation but may be weakened enough for some disease or other insects to attack and kill them. Other defoliators that attack northern red oak are the variable oakleaf caterpillar *(Heterocampa manteo)*, the orangestriped oakworm *(Anisota senatoria)*, and the browntail moth *(Nygmia phaeorrhoea)*. The Asiatic oak weevil *(Cyrtepistomus castaneus)* attacks northern red oak seedlings and has the potential to seriously affect seedling growth because the larvae feed on the fine roots while the adults feed on the foliage.

Much damage is done to northern red oak acorns by the nut weevils *(Curculio* spp.), gall-forming cynipids *(Callirhytis* spp.), the filbertworm *(Melissopus latiferreanus)*, and the acorn moth *(Valentinia glandulella) (7)*. In years of poor acorn production, these insects can destroy the entire crop.

Special Uses

Northern red oak has been extensively planted as an ornamental because of its symmetrical shape and brilliant fall foliage.

The acorns are an important food for squirrels, deer, turkey, mice, voles, and other mammals and birds.

Genetics

Population Differences

Several traits related to geographic origin were identified for northern red oak in a 14-year provenance test in the North- Central States. Time of flushing is earliest for trees of northwestern origin. The trend is then eastward and southward. Autumn leaf coloration is earliest for provenances from northern latitudes and then progresses southward. Provenances from regions at the western edge of the northern red oak range, where periods of high summer temperatures and drought are common, survived better under such conditions than other provenances. Much variation in height growth was present and performance of the provenances was not consistent in all tests. The only consistent difference was the slower growth of the northern provenances in areas farther south. The within-family variation was so great it obscured any real differences in geographic origin *(15)*.

Races

The nomenclature for northern red oak was confused for some time. The scientific names *Quercus borealis* Michx. f. and *Q. borealis* var. *maxima* (Marsh.) Sarg. were adopted after 1915 by some authors, but in 1950, *Quercus rubra* L., the name in universal use before 1915, was restored *(17)*.

Hybrids

Northern red oak hybridizes readily with other species in the subgenus *Erythrobalanus* and the following hybrids have been named: *Quercus* × *columnaris* Laughlin *(Q. palustris* × *rubra)*; *Q.* × *fernaldii* Trel. *(Q. ilicifolia* × *rubra)*; *Q.* × *heterophylla* Michx. f. *(Q. phellos* × *rubra)*; *Q.* × *hawkinsiae* Sudw. *(Q. velutina* × *rubra)*; *Q.* × *riparia* Laughlin *(Q. shumardii* × *rubra)*; *and Q.* × *runcinata* (A. DC.) Engelm. *(Q. imbricaria* × *rubra)*.

Northern red oak also hybridizes with blackjack oak *(Q. marilandica)* and with northern pin oak *(Q. ellipsoidalis) (17)*.

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Quercus shumardii Buckl. Shumard Oak

Fagaceae Beech family

M. B. Edwards

Shumard oak *(Quercus shumardii)* is one of the largest southern red oaks. Other common names are spotted oak, Schneck oak, Shumard red oak, southern red oak, and swamp red oak. It is a lowland tree and grows scattered with other hardwoods on moist, well-drained soils associated with large and small streams. It grows moderately fast and produces acorns every 2 to 4 years that are used by wildlife for food. The wood is superior to most red oaks, but it is mixed indiscriminately with other red oak lumber and used for the same products. This tree makes a handsome shade tree.

Habitat

Native Range

Shumard oak (figs. 1, 2) is found in the Atlantic Coastal Plain primarily from North Carolina to northern Florida and west to central Texas; it is also

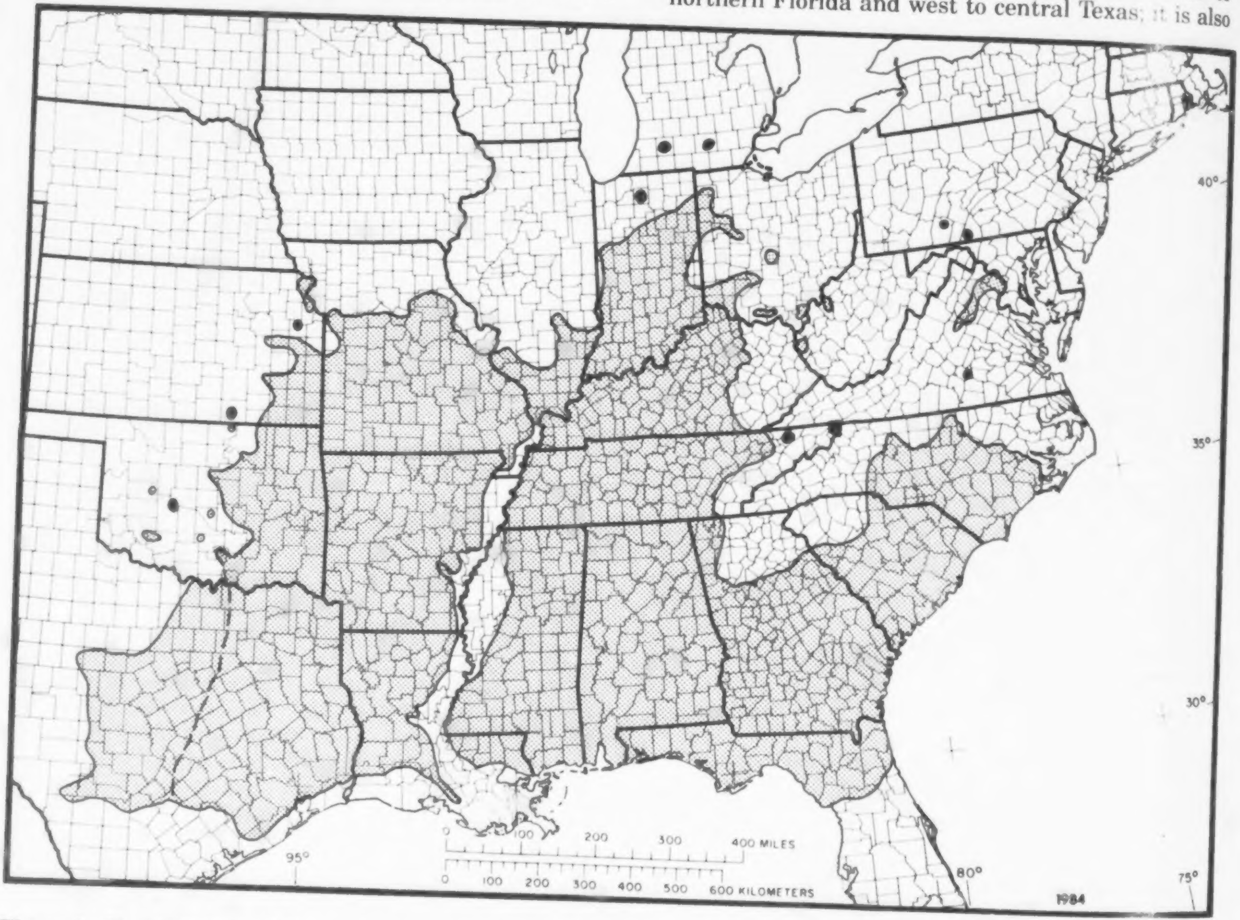

Figure 1—*The native range of Shumard oak,* Quercus shumardii. *The broken line separates eastward the typical variety and westward the variety Texas oak,* Q. shumardii *var.* texana.

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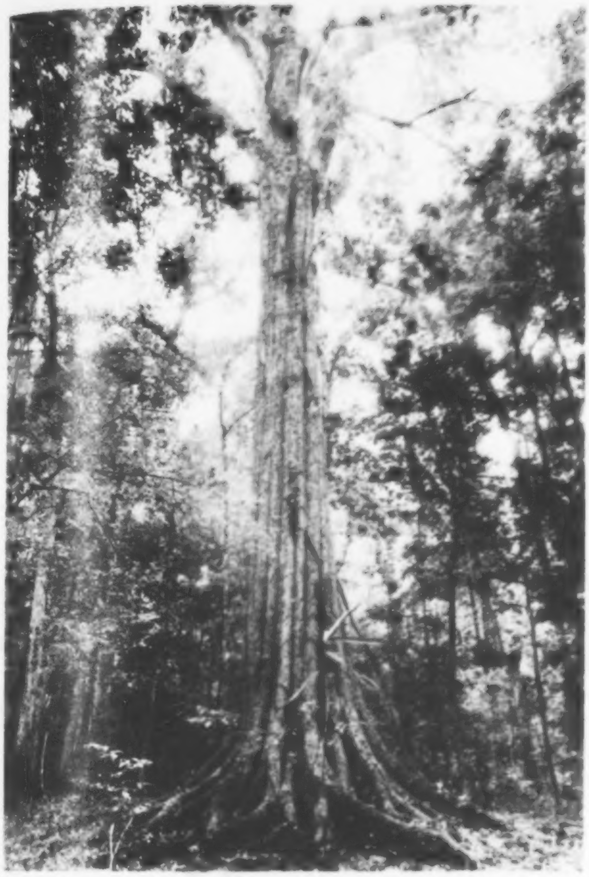

Figure 2—*Shumard oak.*

found north in the Mississippi River Valley to central Oklahoma, eastern Kansas, Missouri, southern Illinois, Indiana, western and southern Ohio, Kentucky, and Tennessee. It is found locally north to southern Michigan, southern Pennsylvania, and Maryland *(4)*.

Climate

Usually Shumard oak grows in a humid, temperate climate, characterized by hot summers and mild, short winters. The growing season usually extends from 210 to 250 days through the major portion of the species commercial range. The average annual temperature is 16° to 21° C (60° to 70° F) with an average annual precipitation of 1140 to 1400 mm (45 to 55 in). The annual maximum temperature for this area is 38° C (100° F) and the annual minimum temperature is about -9° C (15° F). The majority of the rainfall occurs from April through September. Shumard oak tolerates drought well, as shown by its presence in parts of Texas and Oklahoma where the average annual rainfall is only about 640 mm (25 in) *(7)*.

Soils and Topography

Shumard oak grows best in rich sites of the southern forests that have moist, well-drained loamy soils found on terraces, colluvial sites, and adjacent bluffs associated with large and small streams. It is found in hammocks of the Coastal Plain, but rarely on first-bottom sites. It appears to be tolerant of sites with high pH and associated nutrient deficiencies. In trial plantings, Shumard oak has grown well on alluvium with a pH near 7.5. Shumard oak is most commonly found on soils in the orders Alfisols, Inceptisols, and Vertisols.

Associated Forest Cover

Shumard oak is included in the forest cover type Swamp Chestnut Oak–Cherrybark Oak (Society of American Foresters Type 91), a bottom-land type of the Southern Forest Region *(1)*. Shumard oak is a prominent hardwood associate of this type, along with green and white ash *(Fraxinus pennsylvanica* and *F. americana)*, the hickories, shagbark *(Carya ovata)*, shellbark *(C. laciniosa)*, mockernut *(C. tomentosa)*, and bitternut *(C. cordiformis)*, as well as white oak *(Quercus alba)*, Delta post oak *(Q. stellata* var. *paludosa)* and blackgum *(Nyssa sylvatica)*. Main associates in the type are willow oak *(Quercus phellos)*, water oak *(Q. falcata)*, southern red oak *(Q. falcata* var. *falcata)*, post oak *(Q. stellata)*, American elm *(Ulmus americana)*, winged elm *(U. alata)*, water hickory *(Carya aquatica)*, southern magnolia *(Magnolia grandiflora)*, yellow-poplar *(Liriodendron tulipifera)*, beech *(Fagus grandifolia)*, and occasionally loblolly *(Pinus taeda)* and spruce *(P. glabra)* pines.

Shumard oak is often included in cover types Ash–Juniper–Redberry (Pinchot) Juniper (Type 66) and Mohrs (Shin) Oak (Type 67). Some of the other associates of Shumard oak include red buckeye *(Aesculus pavia)*, devils-walkingstick *(Aralia spinosa)*, American hornbeam *(Carpinus caroliniana)*, flowering dogwood *(Cornus florida)*, witch-hazel *(Hamamelis virginiana)*, American holly *(Ilex opaca)*, red mulberry *(Morus rubra)*, southern bayberry *(Myrica cerifera)*, and American basswood *(Tilia caroliniana)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Shumard oak is monoecious. Its flowers usually appear in March or April; they are unisexual, with stamens in glabrous 15 to 18 cm (6 to 7 in) long aments and the pistils are single or paired on pubescent stalks. The fruit is an egg-shaped acorn 2.5 cm (1 in) long, enclosed at the base in a thick, flat, saucer-shaped cup with pubescent scales. The acorn ripens and falls during September or October of its second year.

Seed Production and Dissemination—The minimum seed-bearing age for Shumard oak is 25 years and optimum production is about 50 years. The interval between seed crops is 2 to 3 years. There are about 23 kg (50 lb) of seeds per 35 liters (bushel) of fruit. The range of cleaned seeds per kilogram is 172 to 282 (78 to 128/lb) with an average of 220 (100) *(8)*. Acorns of Shumard oak are an excellent wildlife food and are consumed by birds, white-tailed deer, and squirrels. Animals that hoard the acorns also disseminate them. This species frequently produces multiseeded acorns.

Seedling Development—As with other oaks, germination is hypogeal *(8)*. It appears that the microclimate, edaphic conditions, and several stand variables all have a definite influence on the quantity of small established oak regeneration, but their effect is probably overshadowed by the seed supply. Where oak regeneration is to be favored in uneven-age management, large openings appear most desirable. In even-age management, when a seed-tree cut is contemplated, extremely large- or small-diameter trees should be left as seed producers only as a last resort *(2)*.

The species needs full light to achieve good reproduction. In the Coastal Plain, Shumard oak is found mostly on sites with rich, well-drained soils and an abundance of moisture, but it may also inhabit dry, upland sites.

The stems of the young seedlings are smooth, brownish green or light gray, changing to gray or grayish brown by midseason of the first year. Buds are ovoid with acute apex, 6 mm (0.25 in) long, smooth, with closely overlapping gray-brown or dull straw-colored scales *(5)*.

Vegetative Reproduction—Shumard oak does not propagate readily on moist sites or by cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—Shumard oak grows quite large, especially on favorable bottom-land sites where it reaches a height of 30.5 m (100 ft) or more with a trunk diameter of 0.9 to 1.2 m (3 to 4 ft). Its shape is characterized by a clear trunk and spreading crown. In a report describing the concentration of hardwood species on pine sites, cubic volume is reported for all sites (pine and hardwood) as 7.3 million m^3 (259 million ft^3) in 11 Southern States. The total volume on pine sites is 3.4 million m^3 (120 million ft^3) *(6)*. Heavy pole stands contain over 430 stems/ha (175 stems/acre) 13 to 28 cm (5 to 11 in) d.b.h. In old-growth, mixed stands with Shumard oak, there are total volumes of as much as 420 m^3/ha (30,000 fbm/acre).

Rooting Habit—No information is currently available.

Reaction to Competition—Shumard oak is classed as intolerant of shade and needs open areas as well as adequate moisture to become established; such openings are easily invaded by competing annuals that inhibit oak establishment. It is reported, however, that at maturity Shumard oak retards the growth of competing understory vegetation apparently by an allelopathic effect *(3)*.

Shumard oak reproduction shows some tolerance to complete inundation, a requisite for survival on bottom-land sites. Conditions other than species–site relationships are important in determining the regeneration potential and succession of the species in bottom-land hardwood situations. Water is apparently most likely to become the limiting factor on sites that are consistently flooded for fairly long periods of time during the growing season, such as true swamps, deep sloughs, and backwater areas.

Shumard oak is one of the prominent oaks in oak-hickory regions but does not act as a dominant in the extensive range of the oak-hickory association. Therefore, the place of Shumard oak in the ecological succession is not clearly defined. It is probably not a true climax tree in most oak-hickory communities where it is found.

Damaging Agents—This species is susceptible to wilts and leaf diseases. Oak leaf blister *(Taphrina caerulescens)* is common in certain years. Oak wilt *(Ceratocystis fagacearum)* has killed Shumard oak in Missouri. The most common wood-rotting fungi attacking this oak are *Fomes* spp., *Polyporus* spp., and *Stereum* spp.

No insects are specifically associated with Shumard oak, but many insects attack southern oaks, probably including Shumard. Insect defoliators are June beetles *(Phyllophaga* spp.), orangestriped oakworm *(Anisota senatoria)*, cankerworms *(Alsophila pometaria* and *Paleacrita vernata)*, forest tent caterpillar *(Malacosoma disstria)*, yellownecked caterpillar *(Datana ministra)*, variable oakleaf caterpillar *(Heterocampa manteo)*, and the redhumped oakworm *(Symmerista canicosta)* *(7)*.

The borers that attack healthy trees are red oak borer *(Enaphalodes rufulus)*, in cambium and other sapwood; carpenterworms *(Prionoxystus* spp.), in heart and sapwood; and the Columbian timber beetle *(Corthylus columbianus)*, in sapwood. Those attacking weakened trees include twolined chestnut borer *(Agrilus bilineatus)*, in cambium; and the tilehorned prionus *(Prionus imbricornis)*, in roots.

Dying trees are attacked by the oak timberworm *(Arrhenodes minutus)*. The golden oak scale *(Asterolecanium variolosum)* kills reproduction and tops in older trees. The gouty oak gall *(Callirhytis quercuspunctata)* and horned oak gall *(C. cornigera)* injure small limbs, while the basswood leafminer *(Baliosus nervosus)* attacks the leaves *(7)*.

As in many oaks, the nut is attacked by acorn weevils in the genus *Curculio*. A reliable method of sorting weeviled acorns from sound ones is by color of the cup scar on the nut; a bright, light tan indicates a good acorn, a dull brown, a bad one.

Special Uses

The acorns of Shumard oak serve as mast for numerous species of birds and mammals. In the Mohrs oak and Ashe juniper–redberry juniper types, Shumard oak acorns are probably an important source of food for the deer herd.

Commercially, Shumard oak is marketed with other red oak lumber for flooring, furniture, interior trim, and cabinetry.

Genetics

Shumard oak has two varieties—*Quercus shumardii* Buckl. var. *shumardii* (typical), and *Q. shumardii* var. *texana* (Buckl.) Ashe, Texas oak, found in central Texas, including the Edwards Plateau, and in southern Oklahoma in the Arbuckle Mountains.

Shumard oak hybridizes with *Quercus hypoleucoides; Q. imbricaria* (*Q.* × *egglestonii* Trel.); *Q. marilandica* (*Q.* × *hastingsii* Sarg.); *Q. nigra* (*Q.* × *neopalmeri* Sudw.); *Q. nuttallii; Q. palustris* (*Q.* × *mutabilis* Palmer & Steyerm.); *Q. phellos* (*Q.* × *moultonensis* Ashe); *Q. rubra* (*Q.* × *riparia* Laughlin); and *Q. velutina* (*Q.* × *discreta* Laughlin) *(4)*.

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Quercus stellata Wangenh. **Post Oak**

Fagaceae Beech family

John J. Stransky

Post oak (*Quercus stellata*), sometimes called iron oak, is a medium-sized tree abundant throughout the Southeastern and South Central United States where it forms pure stands in the prairie transition area. This slow-growing oak typically occupies rocky or sandy ridges and dry woodlands with a variety of soils and is considered drought resistant. The wood is very durable in contact with soil and used widely for fenceposts, hence, the name. Due to varying leaf shapes and acorn sizes, several varieties of post oak have been recognized—sand post oak (*Q. stellata* var. *margaretta* (Ashe) Sarg.), and Delta post oak (*Q. stellata* var. *paludosa* Sarg.) are included here.

Habitat

Native Range

The range of post oak (figs. 1, 2) extends from southeastern Massachusetts, Rhode Island, southern Connecticut and extreme southeastern New York (including Long Island); west to southeastern Pennsyl-

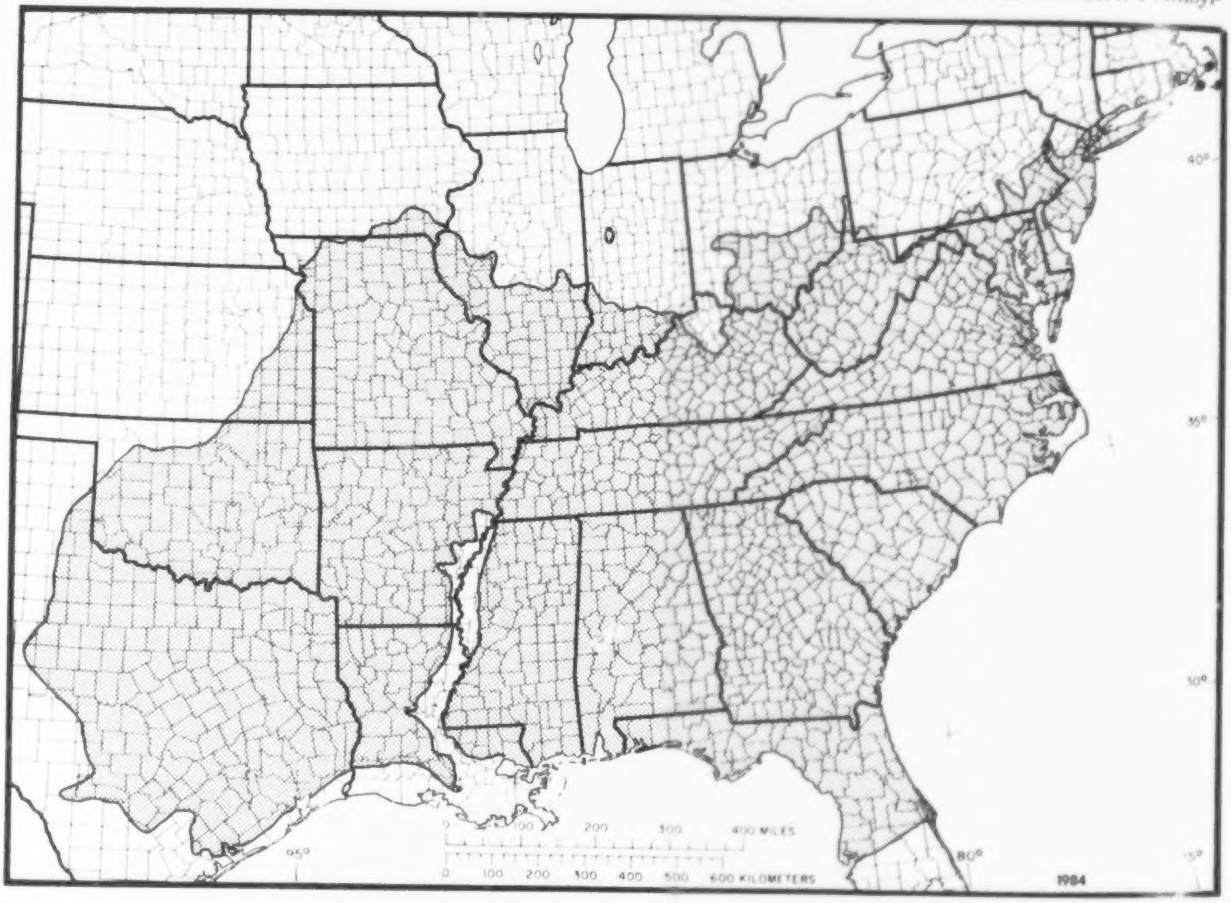

Figure 1—*The native range of post oak.*

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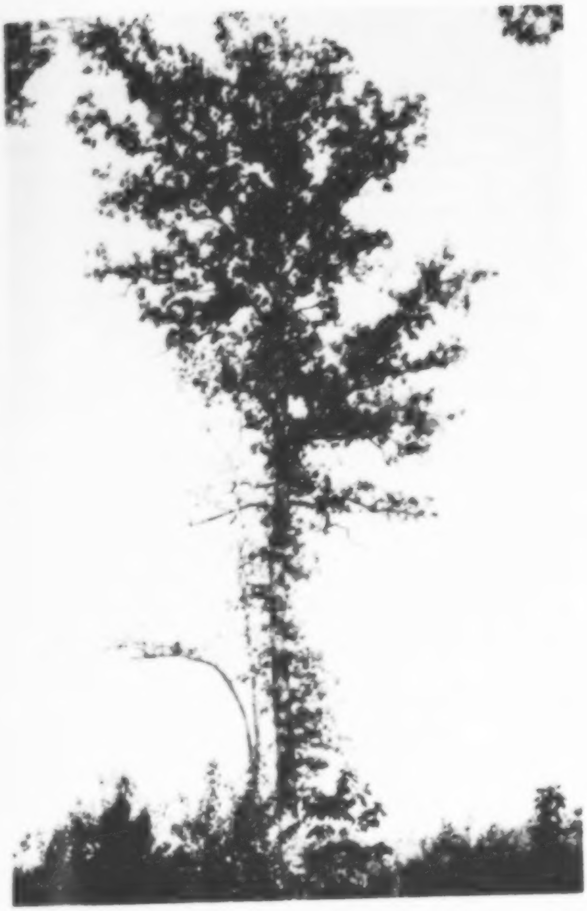

Figure 2—*Post oak left after clearcutting the surrounding loblolly-pine hardwood forest in Nacogdoches County, TX.* (Courtesy J. C. Huntley)

vania and West Virginia, central Ohio, southern Indiana, central Illinois, southeastern Iowa and Missouri; south to eastern Kansas, western Oklahoma, northwestern and central Texas; and east to central Florida *(10)*.

It is a large and abundant tree in the southern Coastal Plain, the Piedmont, and the lower slopes of the Appalachians. It is common in the southwest and grows in pure stands in the prairie transition region of central Oklahoma and Texas known as the "Cross Timbers" *(2)*.

Sand post oak (*Quercus stellata* var. *margaretta* (Ashe) Sarg.) ranges from southeastern Virginia, west to Missouri and eastern Oklahoma, south to central Texas, and east to central Florida. Delta post oak (*Q. stellata* var. *paludosa* Sarg.) is found in bottom lands of the Mississippi River in western Mississippi, southeast Arkansas, and Louisiana, and west to east Texas *(10)*.

Climate

The range of post oak reaches from the humid East to semiarid portions of Oklahoma and Texas. Within this region, average annual precipitation varies from more than 1520 mm (60 in) in west Florida and parts of Louisiana to less than 560 mm (22 in) in central Texas. Annual snowfall varies from 760 cm (30 in) in southeastern Iowa to a trace in Florida *(15)*.

Mean annual temperatures vary from 10° C (50° F) in southern New England and southeastern Iowa to 22° C (72° F) in central Florida. January temperatures average from -6° C (22° F) in southeastern Iowa to 17° C (62° F) in Florida; in July they range from 23° C (73° F) in southern New England to 29° C (85° F) in Texas. Temperature extremes of -11° C (12° F) in Kansas, Oklahoma, and Texas and -40° C (-40° F) in central Missouri have been recorded.

From northwest to southeast the average frost-free period increases from 165 to 300 days, 60 to 90 percent, respectively, of the annual precipitation occurring during this period.

Soils and Topography

Post oak grows on a variety of sites and soils. Its range coincides mostly with that of the Ultisols but also includes some Alfisols in the western portion of its distribution. Typically, it grows on dry sites. Rocky outcrops, ridges, and upper slopes with southerly or westerly exposures are common.

Soils are generally well drained, sandy, coarse textured, deficient in nutrients, and low in organic matter. The surface soil is generally thin but post oak, and especially the scrubby sand post oak, grows on deep sandy, gravelly soils.

Delta post oak grows in fine sandy loam soils on the highest first-bottom ridges in terraces. There is seldom standing water, but the site may be wet due to slow drainage.

Associated Forest Cover

In the Northern Forest Region, post oak is found in the forest cover type White Pine–Chestnut Oak (Society of American Foresters Type 51) *(4)*. On dry ridges and upper slopes its other associates are scarlet, white, and black oaks *(Quercus coccinea, Q. alba,* and *Q. velutina)*, hickories *(Carya* spp.), and pines *(Pinus* spp.).

In the Central Forest Region, post oak is most abundant in Post Oak–Blackjack Oak (Type 40). It extends over a wide area from eastern Kansas south to Texas and east to the Atlantic Coastal Plain. On heavier, clay soils a post oak variant of this type is found, and in the Texas "Cross Timbers" area and in Oklahoma, a post oak savanna. Along with other oaks, post oak is a common associate in several other cover types: Bear Oak (Type 43), Chestnut Oak (Type 44), White Oak–Black Oak–Northern Red Oak (Type 52), White Oak (Type 53), Black Oak (Type 110), Pitch Pine (Type 45), and Eastern Redcedar (Type 46).

In the Southern Forest Region, sand post oak is a chief hardwood component of Sand Pine (Type 69). Sand post oak and post oak grow on drier sites of Longleaf Pine (Type 70) and in Southern Scrub Oak (Type 72). Post oak is a common associate in Longleaf Pine–Slash Pine (Type 83), Shortleaf Pine (Type 75), Virginia Pine (Type 79), Loblolly Pine (Type 81), and Loblolly Pine–Shortleaf Pine (Type 80), and on better drained sites of Slash Pine (Type 84). In the oak-pine types post oak is a common associate in Shortleaf Pine–Oak (Type 76), Virginia Pine–Oak (Type 78), and the Loblolly Pine–Hardwood (Type 82); sand oak is an important component of Longleaf Pine–Scrub Oak (Type 71).

Delta post oak is found in Swamp Chestnut Oak–Cherrybark Oak (Type 91). In Mesquite (Type 68) of east central Texas, post oak appears in mixture with mesquite *(Prosopis* spp.).

The most common hardwoods associated with typical post oak are blackjack oak *(Quercus marilandica)*, black oak, and the hickories. Less common associates include southern red oak *(Q. falcata)*, white oak, scarlet oak, chestnut oak *(Q. prinus)*, shingle oak *(Q. imbricaria)*, live oak *(Q. virginiana)*, chinkapin oak *(Q. muehlenbergii)*, bluejack oak *(Q. incana)*, Shumard oak *(Q. shumardii)*, blackgum *(Nyssa sylvatica)*, sourwood *(Oxydendrum arboreum)*, red maple *(Acer rubrum)*, winged elm *(Ulmus alata)*, hackberry *(Celtis occidentalis)*, chinkapin *(Castanea* spp.), and dogwood *(Cornus* spp.). Coniferous associates are eastern redcedar *(Juniperus virginiana)*, shortleaf pine *(Pinus echinata)*, Virginia pine *(P. virginiana)*, pitch pine *(P. rigida)*, loblolly pine *(P. taeda)*, and occasionally longleaf and slash pines *(P. palustris* and *P. elliottii)*. At higher elevations eastern white pine *(P. strobus)* and hemlock *(Tsuga* spp.) are sometimes associates.

Delta post oak is commonly associated with cherrybark oak *(Quercus falcata* var. *pagodifolia)*, water oak *(Q. nigra)*, willow oak *(Q. phellos)*, swamp chestnut oak *(Q. michauxii)*, white oak, sweetgum *(Liquidambar styraciflua)*, blackgum, American elm *(Ulmus americana)*, winged elm, white ash *(Fraxinus americana)*, hickories, and loblolly pine.

In the South, where post oak is a major component in many stands, the following small trees are common associates: shining sumac *(Rhus copallina)*, smooth sumac *(R. glabra)*, gum bumelia *(Bumelia lanuginosa)*, hawthorns *(Crataegus* spp.), yaupon *(Ilex vomitoria)*, possumhaw *(I. decidua)*, redbud *(Cercis canadensis)*, and rusty blackhaw *(Viburnum rufidulum)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Post oak is monoecious; staminate and pistillate flowers are on the same tree in separate catkins (aments). Flowers appear at the same time as the leaves. Flowering usually begins in March in the South and extends through May further north. Staminate flowers are borne in pendant catkins 5 to 10 cm (2 to 4 in) long. The calyx is yellow, pubescent, and five-lobed; the lobes are acute and laciniately segmented, with four to six stamens and pubescent anthers. Pistillate catkins are short-stalked or sessile and inconspicuous; the scales of the involucre are broadly ovate and hairy with red, short, enlarged stigmas *(18)*.

The acorns mature in one growing season and drop soon after ripening, from September through November. Late freezes after the start of flowering and leafing may cause seed crop failures. The acorns are sessile or short-stalked, borne solitary, in pairs, or clustered; acorns are oval or ovoid-oblong, broad at the base, 13 to 19 mm (0.5 to 0.75 in) long, striate, set in a cup one-third to one-half its length. The cup is bowl-shaped, pale, and often pubescent within. Externally it is hoary-tomentose. The scales of the cup are reddish brown, rounded or acute at the apex, and closely appressed *(18)*.

Seed Production and Dissemination—In common with many other oaks, post oak begins to bear acorns when it is about 25 years old. Good acorn crops are produced at 2- to 3-year intervals; although at several locations in Missouri over a 6-year period, post oak consistently averaged only 200 seeds per tree per year while white, blackjack, black, and scarlet oaks of the same size on the same site bore from 500 to 2,400 acorns per tree. Isolated trees in open fields in east Texas consistently produced well. Elsewhere in Texas, trees less than 15 cm (6 in) in d.b.h. had no acorns *(12)*.

The number of post oak acorns per kilogram averages 838 (380/lb) but may range from 441 to 1,340 (200 to 608/lb) *(17)*.

In a sampling of post oak acorn yields from 736 trees for 18 years (1950–67) in western Louisiana and eastern Texas, the average number of fresh acorns per kilogram was 476 (216/lb) with 39 percent moisture content *(5)*. Mast yield increased linearly with increasing bole size. Expected acorn yield was 1.6 kg (3.6 lb) from trees 30.5 cm (12 in) in d.b.h., and 3.6 kg (8.0 lb) from trees 50.8 cm (20 in) in d.b.h. The percentage of acorn-producing trees also increased with increasing d.b.h. from 42 percent on 15.2 cm (6 in) trees to 76 percent on 55.9 cm (22 in) trees. Expected acorn yield rose from 0.9 kg (2 lb) on trees with a 3.0 m (10 ft) crown diameter to 5.5 kg (12.1 lb) on trees with a 6.1 m (20 ft) crown diameter. Average acorn yield per tree over the 18-year observation period varied from a low 0.03 kg (0.07 lb) in 1962 to a high 4.4 kg (9.7 lb) in 1965.

Seedling Development—Post oak acorns germinate in the autumn soon after dropping. They do not exhibit dormancy. Germination is hypogeal. The best seedbed is a moist soil covered with 2.5 cm (1 in) or more of leaf litter.

Vegetative Reproduction—Post oaks up to 25 cm (10 in) in d.b.h. sprout prolifically after being cut or burned. Along the southwestern margins of its range, post oak spreads rapidly into former grasslands after periodic prairie fires were stopped, and much of this extension appears to be of sprout origin. In one study in which potted seedlings were deprived of moisture until the aboveground parts died, two to three times as many post oaks sprouted after normal moisture was restored than did white, blackjack, northern red, or scarlet oaks *(12)*.

In a comparison of the sprouting habits of five oaks, post oak had more one-stem clumps and fewer sprouts per clump on the average than did black oak, chestnut oak, white oak, or scarlet oak. This characteristic would be important in culture by coppice except that post oak grows more slowly than the others.

Sapling and Pole Stages to Maturity

Growth and Yield—In the Southeast, mature post oaks are from 15.2 to 18.3 m (50 to 60 ft) tall and from 30 to 61 cm (12 to 24 in) in d.b.h. Maximum height rarely exceeds 30 m (100 ft), and diameters exceeding 122 cm (48 in) are uncommon. In the extreme western part of its range, mature trees are seldom larger than 9 to 12 m (30 to 40 ft) tall and 38 to 46 cm (15 to 18 in) in d.b.h. Height and diameter growth for post oak are usually slower than for any of the associated trees except blackjack oak. Ten-year diameter growth generally averages less than 5 cm (2 in), and in central Oklahoma it may be only 13 mm (0.5 in).

Diameter growth of individual post oaks averaging 17 cm (6.7 in) in d.b.h. was stimulated when most of the stand was removed to favor forage production in Robertson County, TX *(12)*. Post oak stands were thinned from an average of 14.9 m^2/ha (65 ft^2/acre) basal area to 8.9, 6.0, and 3.0 m^2/ha (39, 26, and 13 ft^2/acre). In the two ensuing growing seasons, average annual diameter growth for the heaviest thinning was twice that of the uncut check plots (3.6 mm compared to 1.8 mm, excluding bark, or 0.14 in compared to 0.07 in).

Average post oak stands in east Texas contain a volume of about 47.2 m^3/ha (7.5 cords or 675 ft^3/acre). In an Oklahoma woodland, typical of the dry upland post oak type, post oaks 30 cm (12 in) in d.b.h. and larger made up 64 percent of the sawtimber volume (Doyle rule) in a stand averaging nearly 28.0 m^3/ha (2,000 fbm/acre). The average post oak contained 0.4 m^3 (70 fbm).

Rooting Habit—Post oak seedlings have especially thick taproots, usually exceeding the shoot diameter; but overall root development is less than that of northern red *(Quercus rubra)*, scarlet, white, and blackjack oak *(12)*. Although post oak seedlings do become established on sites having a tight clay subsoil, their growth is slow and most roots develop above the underlying clay *(3)*. Post oak seedlings were found to be the most drought resistant of four Missouri oaks, primarily because of the greater drought tolerance of their leaf and root cells *(13)*. In Alabama, post oak was the least tolerant of flooding of all species tested *(6)*.

Reaction to Competition—Post oak is intolerant of competition and is classed as intolerant of shade. Because of its slow height growth it often is overtopped by other trees, including most other oaks. On poor sites, however, post oak tends to persist and become dominant because it is more drought resistant than many of its associates *(12)*.

Damaging Agents—Post oak is susceptible to most insects, diseases, and pollutants that present a threat to other oaks. Regeneration efforts are hampered by acorns being destroyed by weevils. Insect defoliators, leafrollers, tent caterpillars, Gypsy moth, sawfly, leaf miners, and skeletonizers may cause growth losses, and when repeated, may cause mortality *(14)*. The foliage also is susceptible to attacks by aphids, lace bugs, various scales, gall wasps, and mites. The trunk, twigs, and roots may be damaged by carpenterworms, borers, beetles, twig pruners, white grubs, and cicadas (locusts). Some of these cause defects that render the wood unfit for many commercial purposes *(1)*.

Chestnut blight fungus *(Cryphonectria parasitica)* causes many defects as well as mortality to post oak throughout its range *(8)*. The tree also is subject to oak wilt *(Ceratocystis fagacearum)*, a vascular disease prevalent mostly north of the 35th parallel, but not to the same degree as on red oaks. Soil-inhabiting fungi may cause heavy seedling mortality by damping off. Powdery mildews stunt and deform nursery seedlings.

Many fungi produce spots, blotches, blisters, and blights on the foliage. They rarely cause real damage but are unsightly.

Decay fungi cause cankers, rots, and discoloration of the upper and lower stem, as well as of the roots. The Texas root rot *(Phymatotrichum omnivorum)* attacks mainly oaks planted on old farm fields or in subdivisions *(14)*.

Several species of mistletoe are often found on branches and trunks of post oak. Infected branches may be stunted and eventually die. Trees usually are not killed.

Nonpoint source pollutants near large cities cause twigs of many oaks to die back, or kill the trees. The specific diagnosis is usually difficult. Sulfur dioxide, fluoride, ammonia, and some herbicides have been identified as probable agents.

Special Uses

Post oak is a valuable contributor to wildlife food and cover. Acorns provide high energy food during fall and winter and are considered important in the diet of wild turkey, white-tailed deer, squirrels, and many other rodents. When acorns are available animals fatten quickly, go through the winter in good condition, and are most likely to produce healthy young *(7)*. Leaves are used for nest building by birds, squirrels, and raccoons *(11)*. Cavities provide nests and dens for various birds and mammals.

Considered a beautiful shade tree for parks, post oak is often used in urban forestry. It is also planted for soil stabilization on dry, sloping, stony sites where few other trees will grow. It develops an attractive crown with strong horizontal branches. Large trees are difficult to transplant and do not tolerate compaction or removal of soil in developments *(19)*.

The wood of post oak, commercially called white oak, is classified as moderately to very resistant to decay *(16)*. It is used for railroad ties, lathing, siding, planks, construction timbers, mine timbers, trim molding, stair risers and treads, flooring (its highest volume finished products), fenceposts, pulp, veneer, particle boards, and fuel. The bark provides tannin, decorative and protective mulch in landscaping, and fuel.

The tannin in oak leaves, buds, and acorns is toxic to cattle, sheep, and goats. Oak poisoning is a problem in the Southwest where annual livestock losses costing more than $10 million have been estimated. Poisoning occurs more frequently in drought years when other forage is in short supply. The most dangerous season is during the sprouting of new foliage, a period of about 4 weeks in March and April *(9)*.

Genetics

The great variation in post oak and its tendency to hybridize creates a number of varieties and hybrids. The following hybrids with *Quercus stellata* have been recognized *(10)*: *Q. alba (Q.* × *fernowii* Trel.); *Q. bicolor (Q.* × *substellata* Trel.); *Q. durandii (Q.* × *macnabiana* Sudw.); *Q. havardii* (unnamed); *Q. lyrata (Q.* × *sterrettii* Trel.); *Q. macrocarpa (Q.* × *guadalupensis* Sarg.); *Q. minima (Q.* × *neo-tharpii* A. Camus); *Q. mohriana* (unnamed); *Q. prinoides (Q.* × *stelloides* Palmer); *Q. prinus (Q.* × *bernardiensis* W. Wolf); *Q. virginiana (Q.* × *harbisonii* Sarg.).

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Quercus velutina Lam. Black Oak

Fagaceae Beech family

Ivan L. Sander

Black oak (*Quercus velutina*) is a common, medium-sized to large oak of the eastern and midwestern United States. It is sometimes called yellow oak, quercitron, yellowbark oak, or smoothbark oak. It grows best on moist, rich, well-drained soils, but it is often found on poor, dry sandy or heavy glacial clay hillsides where it seldom lives more than 200 years. Good crops of acorns provide wildlife with food. The wood, commercially valuable for furniture and flooring, is sold as red oak. Black oak is seldom used for landscaping.

Habitat

Native Range

Black oak (figs. 1, 2) is widely distributed from southwestern Maine west in New York to extreme southern Ontario, southeastern Minnesota, and Iowa; south in eastern Nebraska, eastern Kansas, central Oklahoma, and eastern Texas; and east to northwestern Florida and Georgia *(18,19)*.

Climate

In the area over which black oak grows, mean annual temperature ranges from about 7° C (45° F) in the north to 20° C (68° F) in east Texas and north-central Florida. Annual precipitation is less than 760 mm (30 in) per year on the northwestern fringe of black oak's range and 2030 mm (80 in) in the southern Appalachians. The frost-free season averages 140 days in southern Wisconsin and 260 days in southeast Texas *(6)*.

Black oak grows best in the Central States where the climate is moderate, with an average annual temperature of 13° C (55° F), precipitation of 1020 to 1270 mm (40 to 50 in), and a frost-free season of about 180 days *(6)*.

Soils and Topography

In southern New England, black oak grows on cool, moist Orthod Spodosols. Elsewhere it occurs on warm, moist soils including Udalf Alfisols, Udoll Mollisols, Udult Ultisols, small areas of Udipsamment Entisols, Dystrochrept Inceptisols, and in extreme northeastern Ohio and northwestern Pennsylvania on Fragiochrept Inceptisols.

The most widespread soils on which black oak grows are the Udalfs and Udolls *(30)*. These soils are derived from glacial materials, sandstones, shales, and limestone and range from heavy clays to loamy sands with some having a high content of rock or chert fragments. Black oak grows best on well-drained, silty clay to loam soils.

Black oak grows on all aspects and slope positions. It grows best in coves and on middle and lower slopes with northerly and easterly aspects. It is found at elevations up to 1200 m (4,000 ft) in the southern Appalachians *(6)*.

The most important factors determining site quality for black oak are the thickness and texture of the A horizon, texture of the B horizon, aspect, and slope position *(2,4,13,20)*. Other factors may be important in localized areas. For example, in northwestern West Virginia increasing precipitation to 1120 mm (44 in) resulted in increased site quality; more than 1120 mm (44 in) had no further effect *(2)*. In southern Indiana, decreasing site quality was associated with increasing slope steepness *(13)*.

Near the limits of black oak's range, topographic factors may restrict its distribution. At the western limits black oak is often found only on north and east aspects where moisture conditions are most favorable. In southern Minnesota and Wisconsin it is usually found only on ridgetops and the lower two-thirds of south- and west-facing slopes *(6)*.

Associated Forest Cover

Black Oak (Society of American Foresters Type 110) is the forest cover type that designates pure stands of the species or those in which it makes up more than 50 percent of the stand basal area. Black oak is a major associate in White Oak–Black Oak–Northern Red Oak (Type 52), and a component in the following forest cover types *(8)*:

Northern Forest Region

14	Northern Pin Oak
51	White Pine–Chestnut Oak
60	Beech–Sugar Maple

Central Forest Region

40	Post Oak–Blackjack Oak
42	Bur Oak
43	Bear Oak
44	Chestnut Oak
45	Pitch Pine

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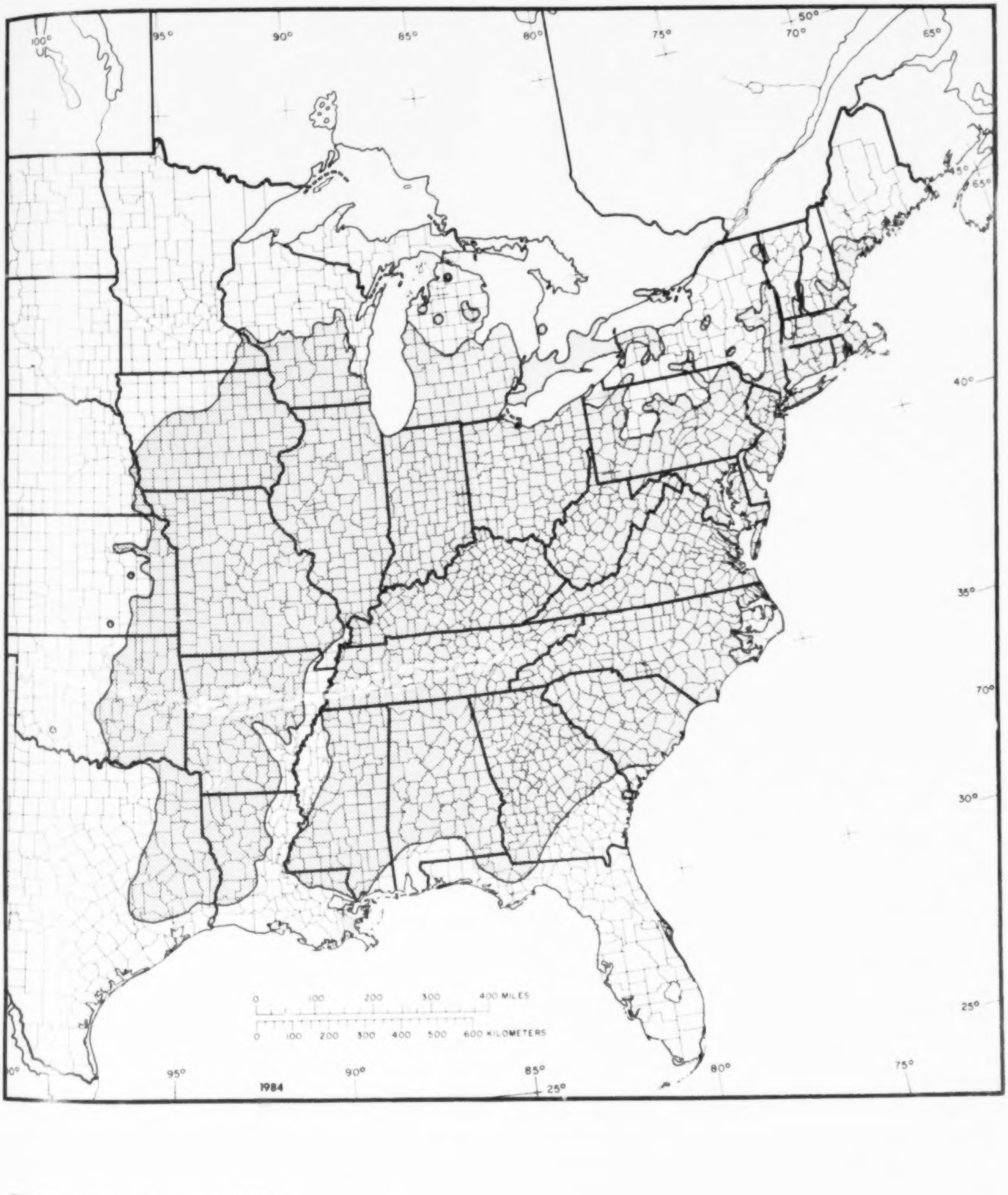
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Figure 1—*The native range of black oak.*

46	Eastern Redcedar
53	White Oak
55	Northern Red Oak
57	Yellow-Poplar
58	Yellow-Poplar–Eastern Hemlock
59	Yellow-Poplar–White Oak–Northern Red Oak

Southern Forest Region

75	Shortleaf Pine
76	Shortleaf Pine–Oak
78	Virginia Pine–Oak
79	Virginia Pine
80	Loblolly Pine–Shortleaf Pine
82	Loblolly Pine–Hardwood

Other tree associates of black oak include pignut hickory *(Carya glabra)*, mockernut hickory *(C. tomentosa)*, bitternut hickory *(C. cordiformis)*, and shagbark hickory *(C. ovata)*; American elm *(Ulmus americana)* and slippery elm *(U. rubra)*; white ash *(Fraxinus americana)*; black walnut *(Juglans nigra)* and butternut *(J. cinerea)*; scarlet oak *(Quercus coccinea)*, southern red oak *(Q. falcata)*, and chinkapin oak *(Q. muehlenbergii)*; red maple *(Acer rubrum)* and sugar maple *(A. saccharum)*; black cherry *(Prunus serotina)*; and blackgum *(Nyssa sylvatica) (5)*.

Common small tree associates of black oak include flowering dogwood *(Cornus florida)*, sourwood *(Oxydendrum arboreum)*, sassafras *(Sassafras albidum)*, eastern hophornbeam *(Ostrya virginiana)*, redbud *(Cercis canadensis)*, pawpaw *(Asimina triloba)*, downy serviceberry *(Amelanchier arborea)*, and American bladdernut *(Staphylea trifolia)*. Common shrubs include *Vaccinium* spp., mountain-laurel *(Kalmia latifolia)*, witch-hazel *(Hamamelis virginiana)*, beaked hazel *(Corylus cornuta)*, spicebush *(Lindera benzoin)*, sumac *(Rhus* spp.), and *Viburnum* spp. The most common vines are greenbrier *(Smilax* spp.), grape *(Vitis* spp.), poison-ivy *(Toxicodendron radicans)*, and Virginia creeper *(Parthenocissus quinquefolia) (5)*.

Life History

Reproduction and Early Growth

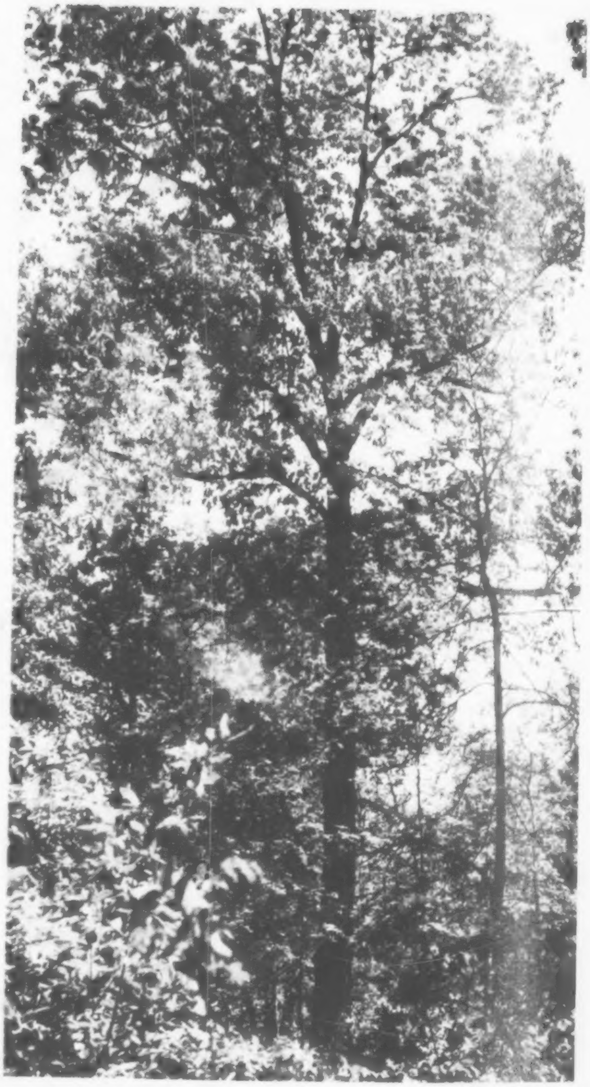

Figure 2—*Black oak.*

Flowering and Fruiting—Black oak is monoecious. The staminate flowers develop from leaf axils of the previous year and the catkins emerge before or at the same time as the current leaves in April or May. The pistillate flowers are borne in the axils of the current year's leaves and may be solitary or occur in two- to many-flowered spikes. The fruit, an acorn that occurs singly or in clusters of two to five, is about one-third enclosed in a scaly cup and matures in 2 years. Black oak acorns are brown when mature and ripen from late August to late October, depending on geographic location *(28)*.

Seed Production and Dissemination—In forest stands, black oak begins to produce seeds at about age 20 and reaches optimum production at 40 to 75 years. It is a consistent seed producer with good crops of acorns every 2 to 3 years. In Missouri, the average number of mature acorns per tree was generally higher than for other oaks over a 5-year period, but the number of acorns differed greatly from year to year and from tree to tree within the same stand *(6)*.

The number of seeds that become available for regenerating black oak may be low even in good seed years. Insects, squirrels, deer, turkey, small rodents, and birds consume many acorns. They can eat or damage a high percentage of the acorn crop in most years and essentially all of it in poor seed years *(6,26)*.

Black oak acorns from a single tree are dispersed over a limited area by squirrels, mice, and gravity *(28)*. The blue jay may disperse over longer distances *(7)*.

Seedling Development—Black oak will be present to the same extent in newly reproduced stands as it was as advance reproduction before harvest cutting. New seedlings established at or just before harvest cutting grow too slowly to compete with sprouts of other tree species and other vegetation *(25,27)*. To compete successfully in new stands black oak stems must be 1.2 to 1.5 m (4 to 5 ft) tall and have well-developed root systems. Success in reproducing black oak depends on creating conditions within mature stands that will result in seedling establishment and conditions favoring their survival and growth *(1,26)*.

Black oak acorns germinate in the spring following seedfall. Germination is hypogeal *(25,28)*. Most favorable conditions for germination occur when the acorns are in contact with or buried in mineral soil and covered with a light layer of litter. Acorns on top of the litter generally dry excessively during early spring and lose their viability before temperatures are favorable for germination. The primary root generally grows vigorously following germination *(6,26)*. Seedlings can survive droughty conditions, but growth is slow or even ceases altogether. Black oak seedlings are more drought tolerant than northern red oak seedlings and about the same as white oak seedlings *(29)*.

Light intensity appears to be critical to the survival and growth of black oak seedlings. Light intensity under forest stands is often very low at the level of the new seedlings (about 15 cm or 6 in). In Missouri, light intensity at this level in forest stands was 10 percent or less of that in nearby open areas. The black oak seedlings in this study averaged 9 cm (3.5 in) tall at age 4, the same as they averaged at age 1 *(26)*.

Black oak seedlings that survive seldom remain true seedlings for more than a few years because drought, low light intensity, fire, animals, or mechanical agents kill the tops. Then, one or more dormant buds near the root collar produce new sprouts. This dieback and resprouting process can occur several times; thus the roots of black oak saplings may be 10 to 20 years older than the tops *(27)*. Growth of black oak sprouts, like that of seedlings, is slow under forest stands. In Missouri, sprouts grew only 6 cm (2.4 in) in 4 years *(26)*.

Shoot elongation of black oak is episodic. Multiple shoot-growth flushes occur in both seedlings and sprouts when light, temperature, and moisture conditions are favorable. Only one growth flush occurs on stems growing in a shaded understory. Periods of active shoot growth are followed by distinctive rest periods, during which most of the annual root elongation occurs *(22)*.

Vegetative Reproduction—About 95 percent of the black oaks in newly reproduced stands created by clearcutting or final overstory removal are sprouts, either from advance reproduction or from stumps of cut trees *(27)*. New sprouts from advance reproduction develop from dormant buds near the root collar when the old stems are cut or damaged during logging. These new sprouts grow rapidly and their height growth is related to the size of the old stem; the larger the old stem, the faster a new sprout will grow *(23,24)*.

Stumps of black oaks sprout less frequently than those of northern red, scarlet, and chestnut oaks and with about the same frequency as those of white oak *(25)*. A Missouri study showed that sprouting frequency for black oak stumps is related to site index, tree age, and stump diameter. Small stumps from young trees on good sites sprout most frequently while large stumps from old trees on poor sites sprout least frequently *(16)*. Black oak stump sprouts grow rapidly: in Missouri the height of dominant and codominant stems averaged 3.5 m (11.4 ft) at age 5. The probability that a stump with a living sprout 1 year old will have at least one dominant or codominant sprout at age 5 is predictable from stump diameter and ranges from near 1.0 for 7.6 cm (3 in) stumps to about 0.15 for 76 cm (30 in) stumps. Black oak stump sprouts may be a valuable component of newly reproduced stands, particularly if they originate at ground level. The low-origin sprouts are less susceptible to rot entering from the parent stump than the high-origin sprouts. Many develop into trees of good quality *(27)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Black oak becomes physiologically mature at about 100 years of age, some individuals living 150 to 200 years. On the best sites black oak trees may reach 46 m (150 ft) in height and 122 cm (48 in) in d.b.h., but most mature trees are 18 to 24 m (60 to 80 ft) tall and 61 to 91 cm (24 to 36 in) in d.b.h. *(6)*.

Average diameter growth of black oak for a range of ages, sites, and stand conditions in the Central States was about 5 mm (0.2 in) per year for 10 years. In West Virginia, dominant black oaks grew faster in diameter than scarlet, chestnut, and white oaks but slower than northern red oak *(6)*.

Average growing space requirements for oaks in even-aged stands in which black oak is a major component have been determined by Gingrich *(9)*. Competition for growing space in these stands begins at the level of stocking where the total available space is equal to the total of the maximum requirement of all the trees in the stand. This level of stocking is about 60 percent of the maximum stocking a site can support and is the lowest level of stocking at which the stand will fully utilize the site. The maximum amount of growing space a black oak tree can use is 33.3 m^2 (358 ft^2) for a tree 20 cm (8 in) in d.b.h. and 115 m^2 (1,233 ft^2) for a tree 51 cm (20 in) in d.b.h. The minimum growing space required for trees is 13.5 m^2 (145 ft^2) and 64.8 m^2 (697 ft^2), respectively.

Yields of unthinned, 80-year-old stands with black oak as a major component range from 75.6 m^3/ha (5,400 fbm/acre) on poor sites (site index 16.8 m (55 ft) at base age 50 years) to 175.0 m^3/ha (12,500 fbm/acre) on good sites (site index 22.9 m or 75 ft). Yields can be increased substantially by thinning regularly. At age 70, stands that are first thinned at age 20, with subsequent thinning at about 10-year intervals, yield from 102.9 m^3/ha (7,350 fbm/acre) on poor sites to 278.3 m^3/ha (19,880/acre) on good sites *(10)*.

Rooting Habit—No information available.

Reaction to Competition—Black oak is classed as intermediate in tolerance to shade. It is less tolerant than many of its associates such as white and chestnut oaks, hickories, beech *(Fagus grandifolia)*, maples, elm, and blackgum; it is more tolerant than yellow-poplar *(Liriodendron tulipifera)*, black cherry, and shortleaf pine *(Pinus echinata)*; and it is about the same as northern red oak and scarlet oak. Seedlings usually die within a few years after being established under fully stocked overstories. Most black oak sprouts under mature stands develop crooked stems and flat-topped or misshapen crowns. After the overstory is removed, only the large stems are capable of competing successfully. Seedlings are soon overtopped. The few that survive usually remain in the intermediate crown class *(6,24,27)*.

Even-aged silvicultural systems satisfy the reproduction and growth requirements of black oak better than the all-aged or uneven-aged selection system *(1,27)*. Under the selection system, black oak is unable to reproduce because of inadequate light. Stands containing black oak that are managed under the selection system will gradually be dominated by more shade-tolerant species.

Black oak responds well to release if the released trees are in the codominant or above-average intermediate crown classes. The best response is obtained if release cuttings or thinnings are begun before a stand is 30 years old. Trees in stands older than 30 years that have always been fully stocked generally have small crowns that have been restricted too long. These are unable to make efficient use of the growing space provided by release or thinnings. Thus response is not as good as in younger stands *(25)*.

Ten years following release in an Arkansas study, diameter growth of 50-year-old black and northern red oak trees averaged 40 percent more than that of unreleased trees. Although the rate of diameter growth increased throughout the 10-year period, response was greater and more apparent in years 5–10.

Dormant buds are numerous on the boles of black oak trees. These buds may be stimulated to sprout and produce branches by mechanical pruning or by exposure to greatly increased light, as by thinning heavily or creating openings in the stand. Dominant trees are less likely to produce epicormic branches than those in the lower crown classes *(6,25)*.

Damaging Agents—Wildfires seriously damage black oak trees by killing the cambial tissue at the base of the trees. This creates an entry point for decay fungi, and the end result is loss of volume because of heart rot. Trees up to pole size are easily killed by fire and severe fires may even kill sawtimber. Many of the killed trees sprout and form a new stand *(6)*. However, the economic loss may be large unless at least some of it can be salvaged.

Oak wilt *(Ceratocystis fagacearum)* is a potentially serious vascular disease of black oak that is widespread throughout the eastern United States. Trees die within a few weeks after the symptoms first appear. Usually scattered individuals or small groups of trees are killed, but areas several hectares (acres) in size may be affected. The disease is spread from tree to tree through root grafts and over larger distances by sap-feeding beetles *(Nitidulidae)* and the small oak bark beetle *(6)*.

Shoestring root rot *(Armillaria mellea)* attacks black oak and may kill trees weakened by fire, lightning, drought, insects, or other diseases. A root rot, *Phytophthora cinnamomi*, may kill seedlings in the nursery. Cankers caused by *Strumella* and *Nectria* species damage the boles of black oak but seldom kill trees. Foliage diseases that attack black oak are the same as those that typically attack species in the red oak group and include anthracnose *(Gnomonia quercina)*, leaf blister *(Taphrina* spp.), powdery mildews *(Phyllactinia corylea* and *Microsphaera alni)*, oak-pine rusts *(Cronartium* spp.), and leaf spots *(Actinopelte dryina) (13)*.

Tunneling insects that attack the boles of black oak and cause serious lumber degrade include the carpenterworm *(Prionoxystus robiniae)*, red oak borer *(Enaphalodes rufulus)*, the twolined chestnut borer *(Agrilus bilineatus)*, the oak timberworm *(Arrhenodes minutus)*, and the Columbian timber beetle *(Corthylus columbianus) (3)*.

The gypsy moth *(Lymantria dispar)* feeds on foliage and is potentially the most destructive insect. Although black oaks withstood a single defoliation, two or three defoliations in successive years killed many trees in New Jersey *(17)*. Other defoliators that attack black oak and may occasionally be epidemic are the variable oakleaf caterpillar *(Heterocampa manteo)*, the orangestriped oakworm *(Anisota senatoria)*, and the browntail moth *(Euproctis chrysorrhoea)*.

The nut weevils *(Curculio* spp.), gall-forming cynipids *(Callirhytis* spp.), filbertworm *(Melissopus latiferreanus)*, and acorn moth *(Valentinia glandulella)* damage black oak acorns.

Special Uses

Black oak acorns are an important food for squirrels, white-tail deer, mice, voles, turkeys, and other birds *(11)*. In Illinois, fox squirrels have been observed feeding on black oak catkins *(14)*. Black oak is not extensively planted as an ornamental, but its fall color contributes greatly to the esthetic value of oak forests.

Genetics

Although races of black oak have not been identified, a study of 14 populations from southern Indiana to northern Michigan revealed morphological differences. Northern populations had smaller acorns with less cup cover, lighter yellow inner bark, smaller winter buds, and a more branching growth form than southern populations *(21)*.

Black oak hybridizes readily with other species in the subgenus *Erythrobalanus*. The following named hybrids with *Quercus velutina* are recognized *(19)*: *Q. coccinea (Q. × fontana* Laughlin); *Q. ellipsoidalis (Q. × palaeolithicola* Trel.); *Q. falcata (Q. × pinetorum* Moldenke); *(Q. × willdenowiana* (Dippel) Zabel); *Q. ilicifolia (Q. × rehderi* Trel.); *Q. imbricaria (Q. × leana* Nutt.); *Q. incana (Q. × podophylla* Trel.); *Q. marilandica (Q. × bushii* Sarg.); *Q. nigra (Q. × demarei* Ashe); *Q. palustris (Q. × vaga* Palmer & Steyerm.); *Q. phellos (Q. × filialis* Little); *Q. rubra (Q. × hawkinsiae* Sudw.); *Q. shumardii (Q. × discreta* Laughlin).

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Quercus virginiana Mill. Live Oak

Fagaceae Beech family

W. R. Harms

Live oak *(Quercus virginiana)*, also called Virginia live oak, is evergreen with a variety of forms, shrubby or dwarfed to large and spreading, depending upon the site. Usually live oak grows on sandy soils of low coastal areas, but it also grows in dry sandy woods or moist rich woods. The wood is very heavy and strong but is little used at present. Birds and animals eat the acorns. Live oak is fast-growing and easily transplanted when young so is used widely as an ornamental. Variations in leaf sizes and acorn cup shapes distinguish two varieties from the typical, Texas live oak *(Q. virginiana* var. *fusiformis* (Small) Sarg.) and sand live oak *(Q. virginiana* var. *geminata* (Small) Sarg.) *(4)*.

Habitat

Native Range

Live oak (fig. 1) is found in the lower Coastal Plain of the Southeastern United States from southeastern Virginia south to Georgia and Florida including the

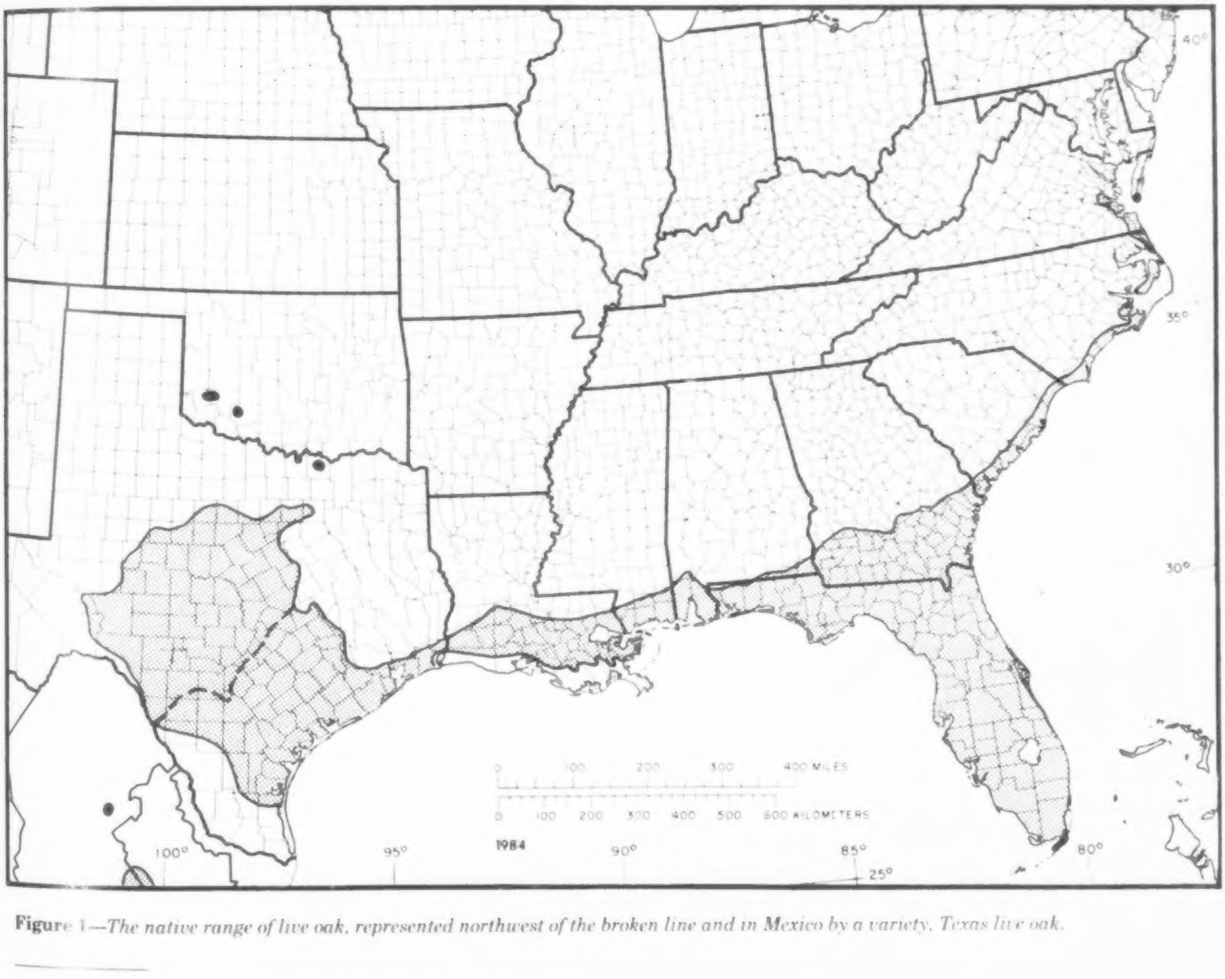

Figure 1—*The native range of live oak, represented northwest of the broken line and in Mexico by a variety, Texas live oak.*

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Florida Keys; west to southern and central Texas with scattered populations in southwestern Oklahoma and the mountains of northeastern Mexico *(4)*.

Climate

The climate is humid. Annual precipitation varies from 810 mm (32 in) in Texas to 1650 mm (65 in) along the Gulf Coast to 1270 mm (50 in) along the Atlantic coast and Florida. During the growing season, March through September, rainfall averages from 460 mm (18 in) in the west to 660 to 760 mm (26 to 30 in) in the east and south, with summer droughts more common in the western part of the range than elsewhere. The average summer temperature is 27° C (80° F). The average winter temperature ranges from 2° C (35° F) in the east and west to 16° C (60° F) in the south. The frost-free period is 240 days in the east and west and more than 300 days in southern Florida *(5)*.

Soils and Topography

Live oak nearly always grows on sandy soils belonging to the Ultisols, Spodosols, Histosols, and Entosols *(5)*. Its resistance to salt spray and high levels of soil salinity makes it a dominant species in the live oak woodland on the barrier islands of the Atlantic and Gulf Coasts. In South Carolina it is found in dry sandy woods, moist rich woods, and wet woods. It is present in nearly every habitat in Florida from sandhills to hammocks, where it is generally the dominant species. In Louisiana, live oak is the dominant species on well-drained ridges bordering coastal marshes *(3)*.

Associated Forest Cover

Live oak makes up the majority of the stocking of the forest cover type Live Oak (Society of American Foresters Type 89) *(1)*. Common associates are water oak *(Quercus nigra)*, laurel oak *(Q. laurifolia)*, southern magnolia *(Magnolia grandiflora)*, and sweetgum *(Liquidambar styraciflua)*. On less well-drained sites it is accompanied by sugarberry *(Celtis laevigata)*, green ash *(Fraxinus pennsylvanica)*, and American elm *(Ulmus americana)*. On the Atlantic Coast and Florida, common associates also include southern bayberry *(Myrica cerifera)*, yaupon *(Ilex vomitoria)*, tree sparkleberry *(Vaccinium arboreum)*, cabbage palmetto *(Sabal palmetto)*, and saw-palmetto *(Serenoa repens)*. American holly *(Ilex opaca)*, flowering dogwood *(Cornus florida)*, southern crab apple *(Malus angustifolia)*, hawthorn *(Crataegus* spp.), pignut hickory *(Carya glabra)*, Carolina jessamine *(Gelsemium sempervirens)*, and Japanese honeysuckle *(Lonicera japonica)* are also common associates.

Live oak is a minor species in seven other forest cover types: Longleaf–Scrub Oak (Type 71), Southern Redcedar (Type 73), Cabbage Palmetto (Type 74), Slash Pine (Type 84), South Florida Slash Pine (Type 111), Ashe Juniper–Redberry Juniper (Type 66), and Mohrs Oak (Type 67).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Live oak is monoecious. Flowers are produced every spring, March through May. The acorns, long and tapered and dark brown to black, mature in September of the first year and fall before December.

Seed Production and Dissemination—Acorn crops are produced annually, often in great abundance. There is no published information on minimum seed-bearing age or size of the acorn crop. Number of sound acorns averages 776/kg (352/lb). Dissemination is by gravity and animals.

Seedling Development—The acorns germinate soon after falling to the ground if the site is moist and warm. Germination is hypogeal. Probably few acorns remain viable over winter because weevils invade them, and they are eaten by many animals and birds. There is no published information on seedling growth and development.

Vegetative Reproduction—Live oak sprouts abundantly from the root collar and roots. When tops are killed or when the tree is girdled, roots near the ground surface send up numerous sprouts. The capacity to sprout makes live oak difficult to kill by mechanical or chemical means.

Sapling and Pole Stages to Maturity

Growth and Yield—Live oak (figs. 2, 3) never attains great height, but the crown may have a span of 46 m (150 ft) or more. Open-grown specimens may have trunks 200 cm (79 in) in d.b.h. and average 15 m (50 ft) in height. Since the species is of little commercial importance except as an ornamental, growth and yield information has never been developed.

Figure 2—*A stand of live oak on Jekyll Island along the Georgia coast.*

Figure 3—*Live oak, 500 to 700 years old, in South Carolina.*

Rooting Habit—There is no published information on rooting habits, but the ability of live oak to grow and mature on sites subject to hurricane-force winds suggests that it is a deep-rooted species.

Reaction to Competition—Live oak may be most accurately classed as intermediate in tolerance to shade. In the northern part of its range, live oak assumes dominance only near the coast, where it is freed from competition by the greater sensitivity of all other broad-leaf trees to salt spray. The exclusion of fire has increased its presence in the Lower Coastal Plain. Once established in a favorable habitat, the tree is very tenacious and withstands all competition.

Damaging Agents—Young live oak is highly susceptible to fire. Its thin bark is readily killed by even light ground fires, leaving the trunk open to insects and fungi. The species is also susceptible to damage by freezing temperatures.

Live oak decline, a wilt disease attributed to *Ceratocystis fagacearum*, has been reported in Texas where it is killing thousands of trees annually. The disease is also suspected to occur in other Southern States as well and is considered a potentially serious problem (*2,3*). Leaf blister, caused by *Taphrina caerulescens*, periodically results in considerable defoliation.

A borer, *Archodontes melanopus*, commonly attacks roots of young oaks on the Atlantic Coast and may prevent the trees from developing normal form.

In some localities, mistletoe (*Phoradendron* spp.) grows on the branches. Spanish moss (*Tillandsia usneoides*), though an epiphyte, may damage trees because it accumulates in great abundance and decreases light reaching the interior and lower parts of the crown (*6*).

Special Uses

Because of live oak's habit of forming a low, widespreading crown, it is widely used as a shade tree and an ornamental. Its acorns are sweet and much sought as food by birds and animals. During the era of wooden ships it was used extensively in shipbuilding because of its hardness and strength.

Genetics

Two varieties of live oak are recognized: *Quercus virginiana* var. *fusiformis* (Small) Sarg., Texas live oak, and *Q. virginiana* var. *geminata* (Small) Sarg., sand live oak.

Live oak hybridizes with *Quercus bicolor* (*Q.* × *nessiana* Palmer); *Q. durandii; Q. lyrata* (*Q.* × *comptoniae* Sarg.); *Q. macrocarpa; Q. minima;* and *Q. stellata* (*Q.* × *harbisonii* Sarg.).

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Robinia pseudoacacia L. Black Locust

Leguminosae Legume family

J. C. Huntley

Black locust *(Robinia pseudoacacia)*, sometimes called yellow locust, grows naturally on a wide range of sites but does best on rich moist limestone soils. It has escaped cultivation and become naturalized throughout eastern North America and parts of the West.

Black locust is not a commercial timber species but is useful for many other purposes. Because it is a nitrogen fixer and has rapid juvenile growth, it is widely planted as an ornamental, for shelterbelts, and for land reclamation. It is suitable for fuelwood and pulp and provides cover for wildlife, browse for deer, and cavities for birds.

Habitat

Native Range

Black locust (figs. 1, 2) has a disjunct original range, the extent of which is not accurately known. The eastern section is centered in the Appalachian Mountains and ranges from central Pennsylvania and southern Ohio, south to northeastern Alabama, northern Georgia, and northwestern South Carolina. The western section includes the Ozark Plateau of southern Missouri, northern Arkansas, and northeastern Oklahoma, and the Ouachita Mountains of

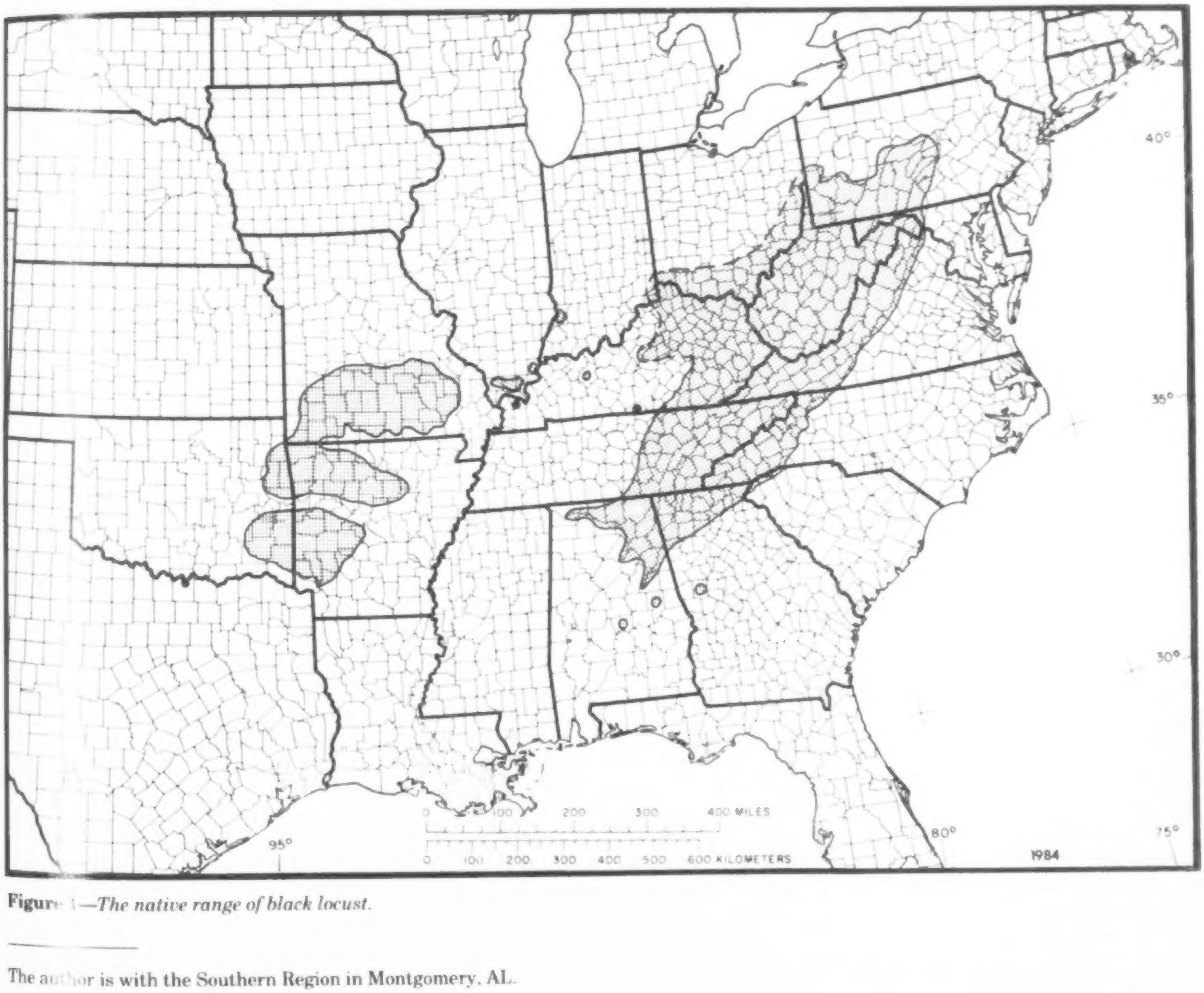

Figure 1—*The native range of black locust.*

The author is with the Southern Region in Montgomery, AL.

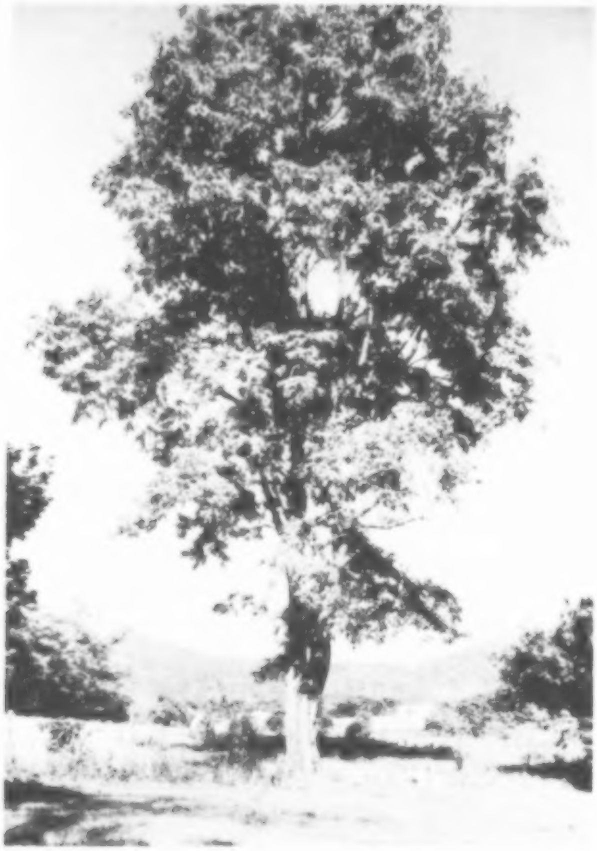

Figure 2—*Black locust.*

central Arkansas and southeastern Oklahoma. Outlying populations appear in southern Indiana and Illinois, Kentucky, Alabama, and Georgia *(26)*. Black locust has been planted widely and has become naturalized throughout the United States, southern Canada, and parts of Europe and Asia.

Climate

The native range of black locust is classified as humid, with two local areas of superhumid climate *(43)*. The range includes the cool temperate moist forest, warm temperate montane moist forest, warm temperate montane wet forest, and warm temperate moist forest life zones *(38)*.

Native black locust appears under the following ranges of climatic conditions *(45)*. January normal daily temperatures: maximum, 2° to 13° C (36° to 55° F); minimum, -7° to 2° C (20° to 36° F); average -4° to 7° C (25° to 45° F); August normal daily temperatures: maximum, 27° to 32° C (81° to 90° F); minimum, 13° to 21° C (55° to 70° F); average, 18° to 27° C (64° to 81° F); mean length of frost-free period, 150 to 210 days; normal annual total precipitation, 1020 to 1830 mm (40 to 72 in); mean annual total snowfall, 5 to 152 cm (2 to 60 in). Black locust has been successfully introduced into many parts of the world where the climatic conditions are different from those of its native range.

Soils and Topography

Black locust grows naturally over a wide range of soils and topography. The most common orders of soil within its native range are Inceptisols, Ultisols, and Alfisols, and the most common soil great groups are Hapludults, Paleudults, Dystrochrepts, and Eutrochrepts *(41)*. The species does best on moist, rich, loamy soils or those of limestone origin and thrives best on moist slopes of the eastern mountains below 1040 m (3,400 ft) *(18,21)*. In the Great Smoky Mountains National Park, the upper elevational limit is 1620 m (5,300 ft) *(46)*. Black locust has become established on a wide variety of disturbed sites such as old fields or other cleared areas.

Black locust is very sensitive to poorly drained or compact plastic soils. Excessively dry sites are also poor for the species. Yellow, brown, or reddish-brown subsoils without pronounced mottling are better than gray, bluish-gray, or yellow subsoils mottled any color. Silt loams, sandy loams, and the lighter textured soils are superior to clay, silty clay loams, and the heavier soils. In the Central States, growth of black locust plantations was found to be closely correlated to plasticity, compactness, and structure of the subsoil, all of which influence drainage and aeration. Growth was unfavorably affected by insufficient or excessive drainage. Soil pH from 4.6 to 8.2 and the amount of mineral nutrients present showed no relationship to growth. Growth was best on limestone-derived soils and soils without pronounced subsoil development *(37)*.

On West Virginia spoil banks, black locust was the most successful species, but survival declined as slope increased. On slopes greater than 25 percent, each 10 percent increase in slope decreased survival 3.4 percent. On slopes steeper than 40 percent, growth was inversely related to slope steepness. Survival was about 80 percent at elevations of 340 to 670 m (1,100 to 2,200 ft). Above 670 m (2,200 ft), survival decreased steadily with increasing elevation and at 1330 m (4,350 ft) survival was less than 65 percent *(7)*.

Although black locust has done well in mine spoil banks in the Central States, it has failed consistently when planted on badly eroded, compacted, clayey soils of the southern Appalachian Region *(21)*. In the Arkansas Ozarks, many plantations on worn out and eroded fields were complete failures. On the southwestern Coastal Plain of Arkansas, plantations on sites previously in agricultural crops failed because of slow growth due to low soil fertility, repeated attacks by the locust borer *(Megacyllene robiniae)*, and invasion of pine *(32)*.

Associated Forest Cover

Black locust develops and grows best in cove or mixed mesophytic forests of the central and southern Appalachian Region. These forests are usually highly productive and characterized by a large and variable number of species. The species is often a component of mature forest on such sites but is seldom very abundant. Black locust is listed as a component of the Mixed Mesophytic Forest *(6)*. In the Cumberland Mountains of Kentucky, it made up about 1 percent of the mixed mesophytic forest on north and south slopes but is considered as more properly belonging to other communities and as a relict from preceding stages or accidentals from nearby unlike communities. It is not listed as a component of oak–hickory forest in the Ozark and Ouachita Highlands or of oak–chestnut forest in the southern Appalachians but is listed as an associate of shortleaf pine *(Pinus echinata)* and Table Mountain pine *(P. pungens)* in the oak–pine communities of the oak–chestnut forest region.

In the forest cover type Black Locust (Society of American Foresters Type 50) the species is in pure stands or makes up the majority of stocking *(15)*. Black locust is listed as an associate in only two other types: Yellow-Poplar (Type 57) and Yellow-Poplar–White Oak–Northern Red Oak (Type 59). Black locust is a pioneer type, usually man-influenced, and temporary. It follows disturbances and may be natural or planted. The type is found locally throughout the Eastern United States and in southern Canada. Black locust makes up a majority of the stand during early stages but is short lived and seldom matures to a sawtimber stand. A wide variety of species become associated with black locust and usually replace most of it. On good sites, single trees or small groups may persist, grow to a large size, and form a small part of the ultimate canopy layer.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The fragrant, whitish flowers, borne in showy racemes, appear after leaf emergence in May or June. The perfect flowers originate in the axils of current year leaves and are pollinated by insects, primarily bees. The fruit is a flattened, oblong pod that ripens during September and October. The fruit opens on the tree and seeds are dispersed from September to April *(34)*.

Seed Production—Black locust begins seed production at about age 6 and produces good crops at 1- to 2-year intervals. Seed production is best between 15 and 40 years of age and continues until age 60. Black locust yields 7 to 15 kg (15 to 33 lb) of seeds per 45 kg (100 lb) of fruit, and seeds average 52,900/kg (24,009/lb) *(34,37)*.

Seedling Development—Because black locust has been widely planted, the proper seed treatment and nursery practices are well described. Dry seeds can be stored and retain their viability for as long as 10 years if placed in closed containers at 0° to 5° C (32° to 41° F). Because seed coats are impermeable, germination must be induced by scarification. Soaking in concentrated sulfuric acid, soaking in boiling or near-boiling water, and mechanical scarification have proved successful. Germination is epigeal *(34)*.

During seedling development, the first leaf appears within a week after germination and is 8 to 10 cm (3 to 4 in) long after 2 months. The young stems are zig-zag, round to slightly angular, and in the latter half of the first year develop pairs of thorns from stipules at the base of leaf petioles *(29)*. Black locust seedlings grow rapidly when planted on good sites and competition is sparse. Control of competition aids in the establishment and growth of seedlings because black locust is intolerant of shade and herbaceous competition. In plantations in the Tennessee Valley, it was a very site-exacting species and grew poorly on severely eroded sites *(1)*. Average annual height growth of 5-year-old plantations ranged from 0.3 m (1.1 ft) on severely sheet-eroded sites to 0.8 m (2.6 ft) on sites with little or no erosion. In the Central States, annual height growth for the first 10 years averaged 0.5 m (1.5 ft) on below-average sites but was 1.2 m (4 ft) or more on good sites *(37)*. Black locust can be established on poor and disturbed sites. It has been widely planted for erosion control along roadsides and for reclamation of surface mine spoil banks. Throughout the Eastern and Central States, reclamation plantings have been successful across a wide range of spoil bank conditions.

Vegetative Reproduction—Black locust sprouts readily from both stump and roots, especially after being cut or damaged. Although seedlings are produced, root suckers are most prevalent in natural reproduction. Suckers usually appear in the fourth or fifth year *(37)*. In the southern Appalachians, dense thickets of suckers develop in clearcuts *(4,28)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Black locust is a medium-sized tree, generally 12 to 18 m (40 to 60 ft) in height and 30 to 76 cm (12 to 30 in) in diameter. On better sites it may reach 30 m (100 ft) in height and 122 cm (48 in) or more in diameter. The bole of open-grown trees is usually short and separates at 3 to 5 m (10 to 15 ft) into several stout branches, but in stands on good sites the bole is often clear and straight *(18,19)*.

Young trees grow very fast on good sites, but the species matures early and growth rate decreases rapidly after 30 years, especially on poor sites (table 1). Sprouts grow more rapidly than seedlings. Average yields from 27-year-old plantations in the Central States were 126 m^3/ha (1,800 ft^3/acre, 1,100 posts/acre, or 4,100 bd.ft./acre). On the best sites, black locust requires 15 to 20 years to produce post-size trees and 30 years to produce 20 cm (8 in) bolts *(37)*. Little information is available on the growth and yield of black locust in natural stands, but numerous studies have documented its early growth in reclamation plantings *(5,7,11,20,37)*. In West Virginia, slope percent, aspect, elevation, and extent of regrading accounted for 60 percent of height growth variation. Estimated annual height growth on surface-mined sites was tabulated *(8)*.

Table 1—Average size of plantation-grown black locust in the Central States *(37)*

	Site index at base age 50 years					
	9.1 m or 30 ft		18.3 m or 60 ft		27.4 m or 90 ft	
Plantation age	D.b.h.	Height	D.b.h.	Height	D.b.h.	Height
yr	*cm*	*m*	*cm*	*m*	*cm*	*m*
10	4	3.7	7	8.2	11	12.8
25	10	7.6	15	14.0	21	20.7
40	—	9.1	—	17.7	27	25.6
yr	*in*	*ft*	*in*	*ft*	*in*	*ft*
10	1.6	12	2.8	27	4.4	42
25	4.1	25	6.0	46	8.4	68
40	—	30	—	58	10.8	84

Early growth information is available for black locust plantations on abandoned fields in the Arkansas Ozarks *(32)*. On the best 11-year-old plantations, heights ranged from 7.8 to 11.5 m (25.7 to 37.8 ft) and diameters ranged from 6.9 to 10.4 cm (2.7 to 4.1 in). Many of the plantations were complete failures, and established plantations were often severely damaged by insects.

Rooting Habit—Black locust ordinarily produces a shallow and wide-spreading root system that is excellent for soil binding but is also capable of producing deep roots. In the arid Southwest, trees may develop vertical roots from 6.1 to 7.6 m (20 to 25 ft) long *(37)*. This deep rooting ability may explain why black locust can grow in arid lands much drier than its native range. Radial root spread is about 1 to 1.5 times tree height *(10)*.

Reaction to Competition—Black locust is very sensitive to competition and is classed as very intolerant of shade *(44)*. It is found in closed forest stands only as a dominant tree. Reproduction is not successful until perturbations create openings in which black locust, because of its rapid juvenile growth, can compete successfully. In open areas, dense herbaceous growth often prevents seedling establishment *(37)*. On spoil banks in Illinois, survival rate of planted black locust was 83 percent on sparsely vegetated sites but was only 31 percent on densely vegetated sites *(5)*.

Except for reclamation, most forest managers consider this tree a weed species and a strong competitor against more desirable species. Two years after clearcutting a mixed hardwood stand from a good site on the southern Cumberland Plateau, 28 percent of all woody stems taller than 1.4 m (4.5 ft) were black locust. Ten years after clearcutting a high-quality hardwood stand in the southern Appalachians, the number of free-to-grow black locust had decreased but it was still the most abundant tree species *(28)*. Dense black locust thickets occupied at least 15 percent of the area and suppressed the growth of more desirable species *(4)*. Frill treatment with 2,4,5-T controlled the thickets. Glyphosate effectively controlled black locust in Christmas tree plantations in Maryland *(17)*.

Damaging Agents—Black locust is severely damaged by insects and disease, probably more than any other eastern hardwood species. Ubiquitous attacks by the locust borer *(Megcallene robiniae)* and by the heart rot fungi *Phellinus rimosus* or *Polyporus robiniophilus* make growing black locust for timber production impractical. Locust borer larvae construct feeding tunnels throughout the wood, and the holes serve as entry points for heart rot fungi that cause extensive wood decay.

Locust borer attacks can begin at a young age and damage can be so extensive that trees are not suitable for fence posts. Many plantations planted in reclamation projects were seriously damaged, but more trees could be used if cut as soon as they reach post or mine-prop size. Slow-growing trees on poor sites are most susceptible to borer attack. On sites where tree vigor is low, repeated attacks often reduce black locust to sprout clumps. Damage to the sprouts is often as severe as in the original stem *(37)*.

Outbreaks of the locust leafminer *(Odontota dorsalis)* occur almost yearly. Black locust trees throughout an entire region are often defoliated, and during years of low rainfall many are killed. Attacks by the locust twig borer *(Ecdytolopha insiticiana)* occur over a wide area and in heavily infested areas seedling mortality may be high. Black locust is attacked by a wide variety of other insects that cause some degree of damage *(3)*.

Common diseases are heart rot and witches' broom disease, caused by a virus, *Chlorogenus robiniae*. In the southern Appalachians most large trees are infected with heart rot and decay of trunk wood is extensive. In the Texas root-rot belt, black locust is extremely susceptible to *Phymatotrichum omnivorum (21)*. In New Brunswick, plantings of black locust are not recommended because of high mortality and dieback of branches caused by *Nectria cinnabarina* and because of superior performance by conifer species *(40)*.

Although black locust is moderately frost hardy in the southern and central Plains, cold weather damage has occurred in the colder parts of its range *(37)*. In the Appalachian region, it is highly susceptible to frost damage *(44)*. Although the species has been reported to be very susceptible to fire damage, researchers concluded that parts of a study area in Illinois would be rapidly converted to black locust thickets if fire was the only management tool used *(2)*.

Special Uses

Although black locust is not an important timber tree in the United States, it is used for a wide variety of products and is planted for many specialized purposes. It is used for fence posts, mine timbers, poles, railroad ties, insulator pins, ship timber, tree nails for wooden ship construction, boxes, crates, pegs, stakes, and novelties. Pulp with satisfactory mechanical properties can be made, particularly by the sulfate process *(35)*. It is also suitable for use in fuel plantations *(14,16)*.

Black locust is widely planted in the United States, Europe, and Asia for erosion control, reclamation of drastically disturbed sites, windbreaks, nurse crops, amelioration of sites, honey production, and ornamental use. Many early plantations on severely eroded old fields were failures, but establishment on spoil banks has been generally successful. Black locust is often broadcast or hydroseeded with a mixture of herbaceous seed. The most commonly used seeding rate is 2.2 to 3.4 kg/ha (2 to 3 lb/acre) *(12)*.

Because of its soil-improving properties, black locust is often planted in mixtures. Many species have been underplanted in black locust stands. Success of such planting has been variable and many factors have to be considered carefully *(37)*. On mine spoil in Illinois, black locust was a valuable nurse crop for black walnut *(Juglans nigra)*, silver maple *(Acer saccharinum)*, and yellow-poplar *(Liriodendron tulipifera)*, but not for cottonwood *(Populus deltoides)*, sweetgum *(Liquidambar styraciflua)*, or Osage-orange *(Maclura pomifera) (25)*. On surface-mined land in Kansas, survival, growth, and form of black walnut were impaired when planted with black locust *(39)*.

Black locust was superior to other hardwoods in developing wildlife habitat on mine spoils. It quickly provided cover, and by 10 to 15 years native vegetation had established a dense undergrowth *(36)*. Its seeds are rated low as wildlife food but are used to a limited extent by Northern bobwhite, other game birds, and squirrels *(30,42)*. White-tailed deer browse the young growth, and a study in the southern Appalachians showed that 92 percent of the sprouts were browsed *(13)*. Because older trees are usually infected with heart rot, woodpeckers often construct cavities in them. Nest cavities of the downy woodpecker, hairy woodpecker, and common flicker have been found *(9)*.

Genetics

Black locust is a variable species. Many cultural varieties have been recognized, especially in Europe. Forty-nine varieties have been tested in Hungary *(23)*, and varieties have been selected that increase wood production 18 to 32 percent and nectar production 74 percent *(31)*. In Korea, numerous studies have been conducted on the development, morphology, and cytological characteristics of spontaneous and colchicine-induced tetraploids of black locust *(24)*. Shipmast locust *(Robinia pseudoacacia* var. *rectissima)*, a clone of unknown origin, is listed by Little as a natural variety *(27)*. After protein analysis and comparison; however, Huang and others consider shipmast locust an ecological variant and believe that it should not be given varietal status *(22)*.

Selection and propagation of trees with superior vigor, form, and resistance to borers have been attempted. The most promising selections were tested

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in several States. Early results indicate significant differences in borer attack between clones and between sites; however, differences were small and may have no practical application *(33)*.

Four hybrids are recognized *(27)*. These are crosses with Kelsey locust, *Robinia kelseyi* Hutch. *(R.* × *slavinii* Rehd.); New Mexico locust, *R. neomexicana* Gray *(R.* × *holtii* Beissn.); clammy locust, *R. viscosa* Vent. *(R.* × *ambigua* Poir.); and bristly locust, *R. hispida* L. *(R.* × *margaretta* Ashe).

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Sabal palmetto (Walt.) Lodd. ex J. A. & J. H. Schult.

Cabbage Palmetto

Palmae **Palm family**

Dale D. Wade and O. Gordon Langdon

Cabbage palmetto *(Sabal palmetto)* is the most northerly and abundant of the native tree palms. Other names sometimes used are Carolina palmetto, common palmetto, palmetto, and cabbage-palm. This medium-sized unbranched evergreen palm commonly grows on sandy shores, along brackish marshes, in seacoast woodlands of Southeastern United States and throughout peninsular Florida. It can tolerate a broad range of soil conditions and is often planted as a street tree. Abundant fruit crops provide a good supply of food to many kinds of wildlife.

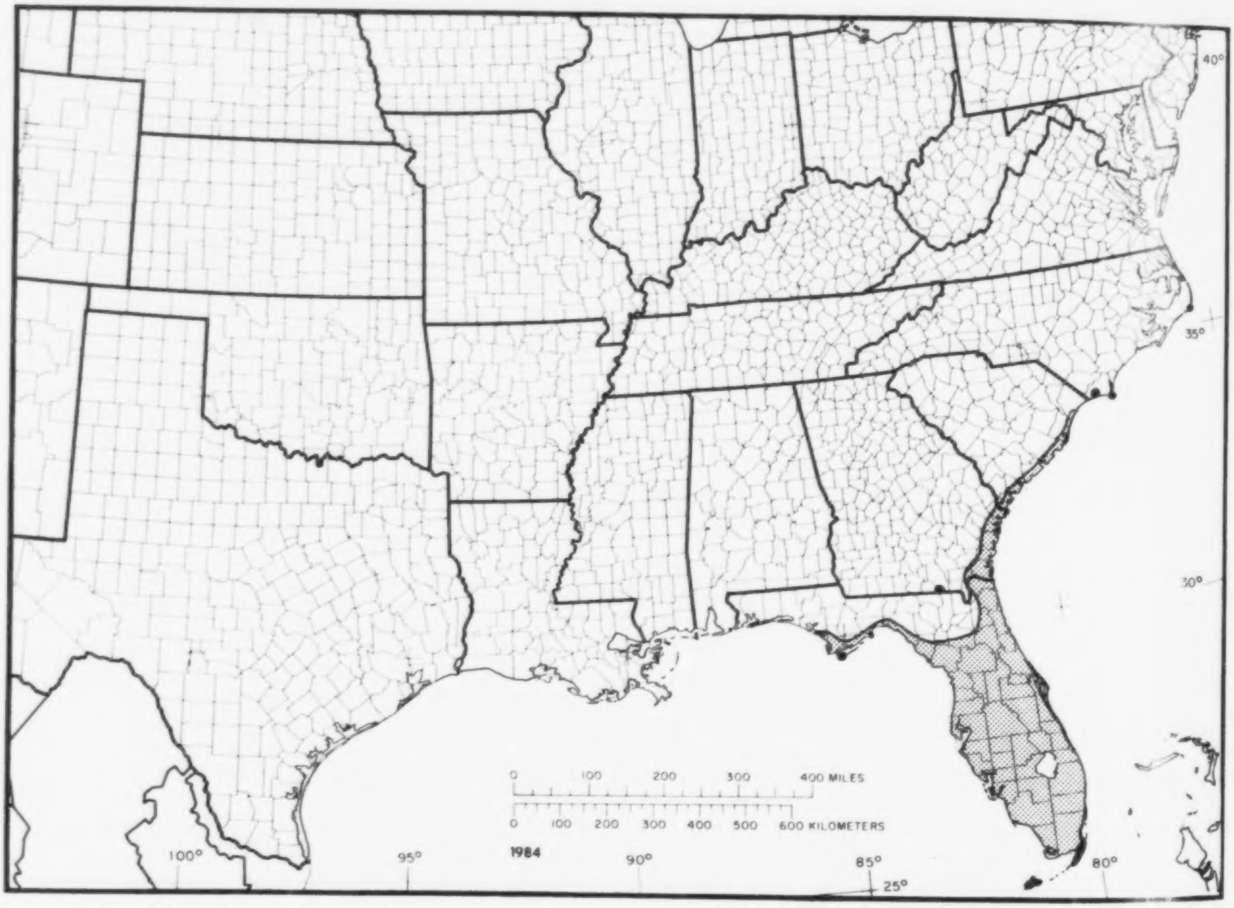

Figure 1—*The native range of cabbage palmetto.*

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Habitat

Native Range

Cabbage palmetto (fig. 1) is the most widely distributed of our native palm trees. Its range extends northward from the Florida Keys through its epicenter in south-central Florida to Cape Fear, NC. A disjunct population has been reported at Cape Hatteras, NC *(16)*. From North Carolina south to the Florida line it hugs the coastline, usually occurring within 20 km (12 mi) of the ocean. In Florida, its northern boundary turns west through Gainesville and follows an ancient shoreline across the peninsula to the Gulf Coast. It then follows the shoreline westward to St. Andrews Bay where its range is slowly extending *(3)*. Outside the United States, it is found in the Bahama Islands *(23)*.

Climate

The climate within the natural range of cabbage palmetto is principally subtropical to warm temperate, humid, with an average annual rainfall of 1000 to 1630 mm (39 to 64 in) and average annual minimum and maximum temperatures from about -4° to 36° C (25° to 97° F). Low winter temperatures apparently limit the horticultural range of the species, which now extends more than 160 km (100 mi) north and inland of its natural range *(3)*.

Soils and Topography

Cabbage palmetto can tolerate a broad range of soil pH, salinity, and drainage but prefers neutral to alkaline soils characterized by near-surface or exposed calcareous sands, marls, or limestone *(10,15)*. Although it grows at the edges of both saline and freshwater areas, it cannot survive lengthy tidal inundations *(8)* but can withstand fluctuations of 2 m (6 ft) in freshwater levels by developing extensive adventitious rootlets along its trunk up to the high-water mark. This cylindrical root mass may reach diameters of 1.8 to 2.4 m (6 to 8 ft) *(24)*.

In the northern part of its range, cabbage palmetto is primarily found on the bay side of coastal dunes and adjacent mainland. Farther south in Georgia, it extends up the flood plains of major rivers. In central Florida, the tree is often found on fine sandy soils with subsoils of limestone or marl on periodically flooded lowlands, and on relic inland dune ridges below 30 m (100 ft), an elevation that defines the approximate shoreline of the Wicomico Sea of the Pleistocene *(7)*. With the construction of drainage ditches in south-central Florida, it has colonized the once seasonally inundated interhammock glades.

The species is found on a wide range of soils including those in the orders Entisols, Alfisols, Ultisols, and Spodosols in south Florida. Drainage tends to be restricted, ranging from somewhat poorly to very poorly drained. All soils appear to have one characteristic in common, a high calcium content, which is indicated by either a high base saturation (Alfisols) or limestone, phosphatic rock, or sea shells in the profile. Soil series typical of the Alfisols are Boca, Bradenton, Parkwood, and Riviera. Typical Entisols are exemplified by the Pompano series. Charlotte, Oldsmar, and Wabasso soil series are typical Spodosols on which the species is found.

The species often forms pure stands up to about 10 ha (25 acres) in freshwater areas, called river hammocks if they lie along a river, and cabbage-palm hammocks or palm savannas if they are on inland prairies.

Associated Forest Cover

In the forest cover type Cabbage Palmetto (Society of American Foresters Type 74), the species usually makes up a plurality of the stocking *(11)*. Because cabbage palmetto can accommodate a wide range of sites, it is found in association with many plant species, especially in south Florida. It is found on severe sites such as dunes, salt flats, barrier islands, cactus thickets, and wet prairies. It is a common component of such diverse communities as freshwater cypress swamps, relic inland dune ridges, and rockland pine forests, where it grows with South Florida slash pine *(Pinus elliottii* var. *densa)* and various tropical hardwoods on limestone outcrops. Other coniferous associates include typical slash pine *(P. elliottii* var. *elliottii)*, pond pine *(P. serotina)*, and loblolly pine *(P. taeda)* at edges of marshes; longleaf pine *(P. palustris)* on dry sites such as xeric hammocks; and eastern redcedar *(Juniperus virginiana)* in hydric hammocks. Cabbage palmetto is also a component of both temperate and subtropical hardwoods, which include species such as the various evergreen oaks *(Quercus* spp.), loblolly-bay *(Gordonia lasianthus)*, redbay *(Persea borbonia)*, magnolias *(Magnolia* spp.), sweetgum *(Liquidambar styraciflua)*, red maple *(Acer rubrum)*, baldcypress *(Taxodium* spp.), pignut hickory *(Carya glabra)*, gumbo-limbo *(Bursera simaruba)*, cocoplum *(Chrysobalanus icaco)*, Florida strangler fig *(Ficus aurea)*, Florida poisontree *(Metopium toxiferum)*, and wild tamarind *(Lysiloma latisiliquum)*. The abundance of cabbage palmetto within a given community is often related to the site's fire history. Cabbage palmetto (fig. 2) can survive fires that kill other arborescent vegetation be-

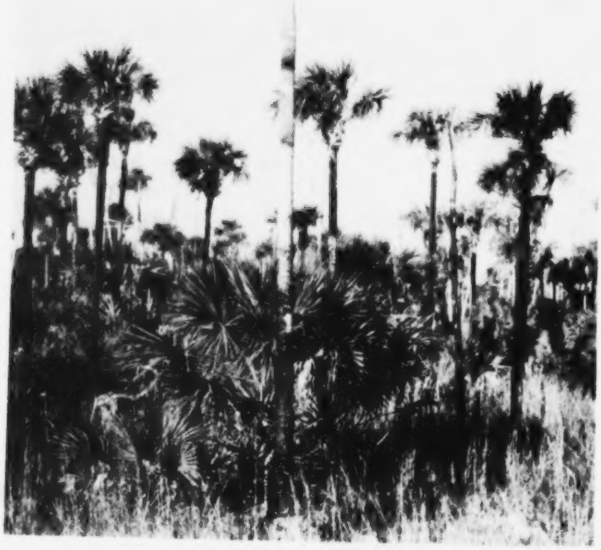

Figure 2—*Cabbage palmetto, shown dominating a cypress–south Florida slash pine forest following frequent fires. Note the fire-killed cypress snags in the background (Collier County, FL).*

cause of its deeply embedded bud and fire-resistant trunk; it thus tends to form pure stands with periodic burning *(19,27,30)*.

Associated understory vegetation includes gallberry *(Ilex glabra)*, huckleberries *(Gaylussacia* spp.) blueberries *(Vaccinium* spp.), lyonias *(Lyonia* spp.), waxmyrtle *(Myrica cerifera)*, holly *(Ilex* spp.), saw-palmetto *(Serenoa repens)*, greenbriar *(Smilax* spp.), bracken *(Pteridium* spp.), blackberry *(Rubus* spp.), poison-ivy *(Toxicodendron radicans)*, bluestem *(Andropogon* spp.), sawgrass *(Cladium jamaicensis)*, beak-rush *(Rhynchospora* spp.), and such epiphytic plants as the common tree orchid *(Tillandsia* spp.), and various bromeliads in the subtropical hammocks.

Several naturalized exotics, namely casuarina *(Casuarina* spp.), melaleuca *(Melaleuca quinquenervia)*, coconut *(Cocos nucifera)*, and Brazil peppertree *(Schinus terebinthifolia)*, are now commonly associated with cabbage palmetto—apparently at its expense—but it is too early to judge the extent of their competition.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowers are perfect, about 6 mm (0.25 in) in diameter by 3 mm (0.125 in) long, and creamy to yellowish white *(19,29)*. The showy flowers are borne in profusion in arching or drooping clusters 1.5 to 2.5 m (5 to 8 ft) long, from April through August in south Florida but for only a 4- to 6-week period beginning in the middle of July in North Carolina *(3,31)*. The fragrant flowers are pollinated by bees, although other insects may be of local importance *(3)*. The fruits are black, fleshy, drupelike berries, 5 to 13 mm (0.2 to 0.5 in) in diameter and averaging about 10 mm (0.4 in), each containing a single, hard, brown, spherical seed *(2,3)*.

Seed Production and Dissemination—The fruits mature in the fall and persist on the spadix until removed by wind, rain, or birds such as ring-billed gulls, fish crows, cardinals, and blue jays. Once on the ground, the fruits are eaten by numerous animals or cached by rodents; such caches result in dense patches of seedlings *(3,14,19)*. In near-coast situations, however, the major means of dissemination appears to be by water. The distribution of cabbage palmetto along the Atlantic shoreline is attributed to the seed's buoyancy and tolerance of saltwater. Thus, the range of cabbage palmetto is a function of the speed and direction of estuarine and littoral currents along a shoreline. This fact explains the species spread northward along the Atlantic Coast and its expansion westward along the Gulf Coast *(3)*.

Cabbage palmetto produces large numbers of fruits and seeds each year. In a cabbage-palm hammock in southwest Florida, an estimated 1,530,000/ha of ripe fruits (620,000/acre) were produced per year, of which 9 percent contained intact seeds after 6 months, 1 percent were infested by beetles, and 89 percent had been totally consumed or removed from the site *(19)*.

Predation of cabbage palmetto seeds by a bruchid beetle *(Caryobruchus gleditsiae)* is the major cause of seed loss and regeneration failure *(3,32)*. When seeds are carried off by animals, the probability of predation by this insect is greatly reduced. Seeds falling into water also escape this predation because they tend to be covered by sand or organic debris, so that germination occurs when temperature and moisture conditions become favorable. However, infestation of the fruit while still on the tree is substantial and can reach 98 percent *(5)*. Seeds exposed to the sun for long periods do not germinate well *(3)*.

Germination of cabbage palmetto seeds is hastened by stratification in moist sand for 30 days at 3° C (37° F) *(18)*. Dormancy is also broken if the micropyle cap is removed. For example, germination of untreated seed was 36 percent in 100 days but was increased to 84 percent or more in 4 days by removal of the micropyle cap *(29)*. Moisture and temperature requirements for germination are satisfactorily met throughout its range. Although the species does not reproduce on the fore dune or beach face, substrate salinity levels encountered on the lee side of dunes or in upper reaches of tidal creeks and marshes do not represent an establishment problem *(3)*.

Seedling Development—Germination of cabbage palmetto is hypogeal. Like other palms, it grows upward from a single terminal bud and outward from the fibrovascular bundles distributed throughout its trunk. Because seeds germinate from middle to late summer, seedling growth the first year normally consists of a primary root, one fully expanded leaf with stem growth obliquely downward forming the rhizome. Ecotypic differences between northern and southern seed sources in seedling photosynthetic and biomass growth rates have been observed *(3)*.

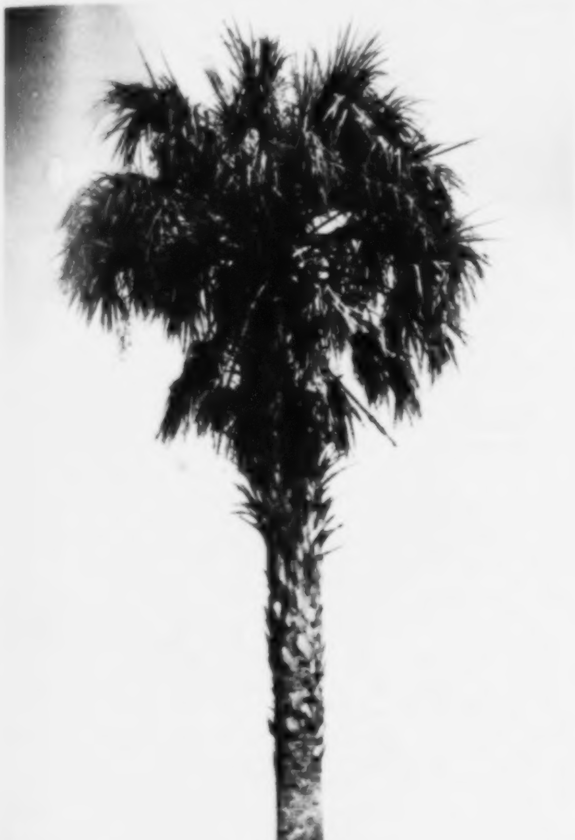

Figure 3—*Cabbage palmetto with boots still attached (Lee County, FL).*

Vegetative Reproduction—No information available.

Sapling and Pole Stages to Maturity

Growth and Yield—Since palms do not have a cambium as such, they do not produce annual growth rings. Cabbage palmetto reaches its maximum development in south-central Florida, but good growth also occurs along the Gulf Coast to the Apalachicola River. Mature trees are straight, unbranched, with heights from 10 to 25 m (33 to 82 ft) and diameters of 30 to 61 cm (12 to 24 in) *(21)*. A dense well rounded crown is almost always formed. On many trees the leaf bases or "boots" remain securely attached while on others they slough off, leaving a fairly smooth trunk (fig. 3). Diameters are exaggerated when these boots remain attached to the trunk. Average growth rates are unknown. One specimen, planted as an ornamental in south-central Florida, grew to a height of 9 m (30 ft) and a diameter including boots of about 76 cm (30 in) in 16 years *(6)*.

Few stand measurements of cabbage palmetto have been made; stem counts, in the rockland pine forest of Everglades National Park *(28)* and in the sandy marl pine-palm association *(4)* and the mixed swamp forest of the Big Cypress National Preserve *(27)*, showed cabbage palm to be rather abundant, with stems numbering 900/ha (364/acre), 500/ha (202/acre), and 180/ha (73/acre), respectively. In a cabbage-palm hammock just north of the Big Cypress Swamp, the count of cabbage palmetto was 1,010/ha (409/acre), with a basal area of 53.0 m^2/ha (231 ft^2/acre); there were 7,150 palm seedlings per hectare (2,895/acre) under breast height *(19)*.

Rooting Habit—The underground stem of cabbage palmetto is short and bulbous, surrounded by a dense mass of contorted roots commonly 1.2 to 1.5 m (4 to 5 ft) in diameter and 1.5 to 1.8 m (5 to 6 ft) deep. From this mass, tough, light-orange roots often almost 13 mm (0.5 in) in diameter penetrate the soil for a distance of 4.6 to 6.1 m (15 to 20 ft) *(22)*.

Reaction to Competition—Cabbage palmetto is classed as shade tolerant and is probably a climatic climax as well as a fire climax. Since intensive management of cabbage palmetto has not been tried, the effects of various silvicultural treatments are conjectural. But its management would appear to be simple and straightforward, with the tree managed in either pure or mixed stands under either an even- or all-age management system.

Damaging Agents—In its native environment, only a rising sea level, hurricanes, and organic soil fires are harmful to this species. It is apparently free of damaging insects and most other pathogens, although bole cankers have been reported *(26)*. Seed predation by the bruchid beetle, as previously discussed, would be a major problem but for the large number of seed produced each year.

South of the Tamiami Trail, which crosses the lower part of south Florida, cabbage palmetto mortality is significant because extensive drainage schemes, resulting in a reduced freshwater head, have combined with a rising sea level to produce increased salinities *(1,8)*. Cabbage palmetto has been rated the most wind-resistant south Florida tree but it nevertheless suffered extensive damage from Hurricane Donna in 1960, particularly on Palm Key in Florida Bay *(9)*. Cabbage palmetto growing on organic soil or deep humus deposits are killed by fire burning in this organic layer because of root mortality and loss of mechanical support. The extensive use of these trees in urban landscaping is depleting native stands of mature cabbage palmetto, suggesting a future need to manage stands for this use.

Special Uses

Cabbage palmetto is so called because of its edible terminal bud which tastes somewhat like that vegetable. The bud, also called swamp cabbage, is good both raw and cooked and is commercially canned and sold. Removal of the bud kills the tree, however. Cabbage palmetto was an important tree to the Seminole Indians, who often made their homes on cabbage-palm hammocks *(23)*. They made bread meal from the fruit, which has a sweet, prunelike flavor, and they used the palm fronds to thatch their chickees (huts) and to make baskets *(10,22,25)*. Many other uses of this tree are documented *(17,22,26)*: pilings for wharfs because they resist attacks by seaworms, stems, hollowed out to form pipes for carrying water, ornamental table tops from polished stem cross-sections, canes, scrub brushes from the bark fibers and leaf sheaths, and logs for cribbing in early fortifications because they did not produce lethal splinters when struck by cannonballs.

Currently, young cabbage palmetto fronds are collected and shipped worldwide each spring for use on Palm Sunday. This tree is in flower when many other plants are not and is a significant source of a strong but delicious dark-amber honey.

Perhaps the most important uses are as an ornamental and as wildlife food. The sheer magnitude of its annual fruit crop is such that it provides a substantial part of the diet of many animals such as deer, bear, raccoon, squirrel, bobwhite, and wild turkey *(12,13,18,19,20)*.

Genetics

The only available information on varieties pertains to growth differences between seedlings at Smith Island, NC, and Miami, FL. Both the biomass and the photosynthetic rate of the Miami seedlings were more than twice that of the Smith Island plants, differences that were statistically significant *(3)*.

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Salix nigra Marsh. **Black Willow**

Salicaceae **Willow family**

J. A. Pitcher and J. S. McKnight

Black willow *(Salix nigra)* is the largest and the only commercially important willow of about 90 species native to North America. It is more distinctly a tree throughout its range than any other native willow; 27 species attain tree size in only part of their range *(3)*. Other names sometimes used are swamp willow, Goodding willow, southwestern black willow, Dudley willow, and sauz (Spanish). This short-lived, fast-growing tree reaches its maximum size and development in the lower Mississippi River Valley and bottom lands of the Gulf Coastal Plain *(4)*. Stringent requirements of seed germination and seedling establishment limit black willow to wet soils near water courses *(5)*, especially floodplains, where it often grows in pure stands. Black willow is used for a variety of wooden products and the tree, with its dense root system, is excellent for stabilizing eroding lands.

Habitat

Native Range

Black willow (fig. 1) is found throughout the Eastern United States and adjacent parts of Canada and Mexico. The range extends from southern New Brunswick and central Maine west in Quebec, southern Ontario, and central Michigan to southeastern Minnesota; south and west to the Rio Grande just below its confluence with the Pecos River; and east along the gulf coast, through the Florida panhandle and southern Georgia. Some authorities consider *Salix gooddingii* as a variety of *S. nigra*, which extends the range to the Western United States *(3,9)*.

Climate

The climate in which black willow grows best is characterized by an average rainfall of 1300 mm (51 in). Approximately 500 mm (20 in) of this occurs during the effective growing season, April through August. The average maximum temperature is 34° C (93° F) in the summer and 15° C (59° F) in the winter. In parts of its range, black willow survives extremes of 46° to -50° C (115° to -58° F). Geographic distribution appears to be independent of temperature *(4,7)*.

Soils and Topography

Black willow is most commonly associated with the soil order Entisols, particularly the Haplaquents and Fluvaquents derived from alluvium. Willow grows on almost any soil, but its extensive, shallow roots need an abundant and continuous supply of moisture during the growing season.

The species is most common on river margins and batture land, where it occupies (and usually dominates) the lower, wetter, and often less sandy sites. It is also common in swamps, sloughs, and swales, and on the banks of bayous, gullies, and drainage ditches, growing anywhere light and moisture conditions are favorable. It flourishes at, or slightly below, water level and is not appreciably damaged by flooding and silting *(4)*.

Although prevalent along most of the Mississippi River, it produces the largest and best formed trees on very low, moist sites in the batture of the lower river.

Associated Forest Cover

Black willow is the predominant species in Black Willow (Society of American Foresters Type 95), a temporary, pioneer forest cover type with excellent growth characteristics *(1)*. It is an associated species in the following cover types: River Birch–Sycamore (Type 61), Cottonwood (Type 63), Sycamore–Sweetgum–American Elm (Type 94), Baldcypress (Type 101), Baldcypress–Tupelo (Type 102), Water Tupelo–Swamp Tupelo (Type 103), and Cottonwood–Willow (Type 235).

Other noteworthy tree associates are red maple *(Acer rubrum)*, boxelder *(A. negundo)*, red mulberry *(Morus rubra)*, and water locust *(Gleditsia aquatica)*. In the areas where willow develops best, swamp-privet *(Forestiera acuminata)*, buttonbush *(Cephalanthus occidentalis)*, and water-elm *(Planera aquatica)* are the major noncommercial tree associates. Black willow often starts with sandbar willow *(Salix exigua)*, which dies out before reaching more than small pulpwood size.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Black willow is dioecious. No consistently reliable morphological charac-

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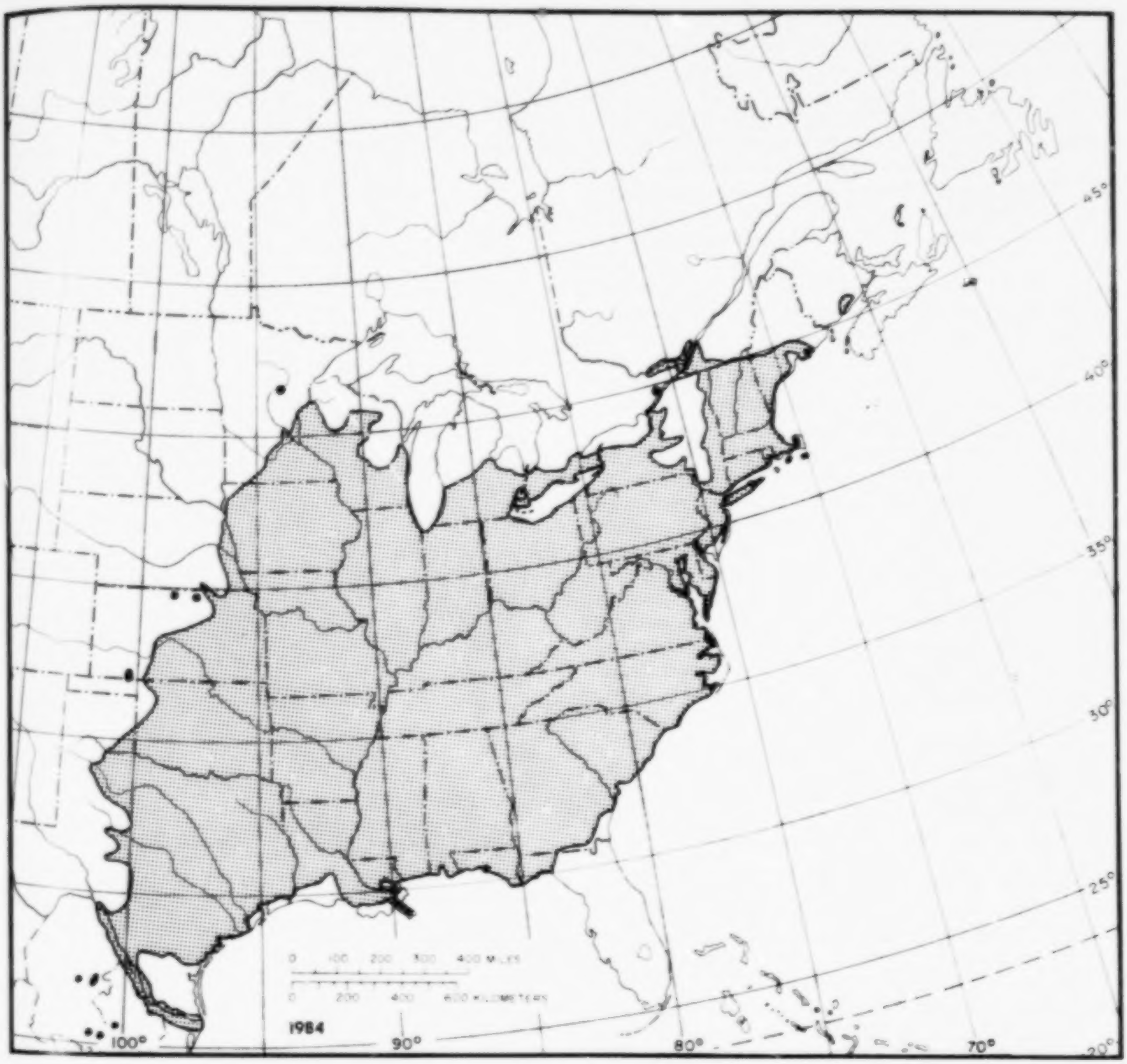

Figure 1—*The native range of black willow.*

teristics are associated with the identification of the sexes. Male and female are indistinguishable except during flowering and seed development. In natural stands the sex ratio is probably 1 to 1, as has been determined for other dioecious tree species, including members of *Salicaceae*. Flowering begins in February in the southern portion of the range and extends through late June at the northern limits. The many-flowered catkins usually appear at the time of or immediately preceding leafing out. Pollination is mainly by insects; the flowers contain nectar. Pollen is also carried by winds. The seed ripens quickly; 45 to 60 days after pollination the small (3 to 6 mm or 0.12 to 0.24 in) light-brown capsules begin to split open and shed minute green seeds that have a hairy covering.

Seed Production and Dissemination—Seed production usually starts when the trees are about 10 years old, although viable seeds can be obtained at younger ages. Optimum seed-bearing age is from 25 to 75 years. The trees have good seed crops almost every year, with only a few interspersed poor crops and rare failures resulting from late freezes after flower buds have begun to open. Large volumes of seeds are produced; they average 5 million/kg (2.3 million/lb). When the seeds fall, the long silky hairs act as wings to carry the seeds very long distances. The seeds are widely disseminated by wind and water.

Seedling Development—Unless the willow seed is floating on water, it must reach the seedbed within 12 to 24 hours because viability is greatly reduced by only a few days of dry conditions. Germination is epigeal. Germinative capacity is usually high and no dormancy is known. Very moist, almost flooded exposed mineral soil is best for satisfactory germination and early development. Full light promotes vigorous growth once the seedling is well established. In a favorable environment, seedlings grow rapidly—often exceeding 1.2 m (4 ft) in height the first year *(4)*.

Seedlings grow best when there is abundant moisture available throughout the growing season. In the Mississippi Valley, average heights are 9.8 m (32 ft) and average breast-high diameters are 6.6 cm (2.6 in) when the saplings are 5 years old *(4)*.

Vegetative Reproduction—Root stocks of very young willow trees sprout prolifically. Propagation by cuttings is the usual method of artificial regeneration. With adequate moisture, good cuttings, and sufficient cultivation to reduce competition from other vegetation, first-year plantation survival can be close to 100 percent. Post-size willow cuttings have been rooted for use in flood projects to prevent gullies *(4)*.

Sapling and Pole Stages to Maturity

Growth and Yield—In natural stands of the lower Mississippi Valley, 10-year-old trees average 15 m (49 ft) in height and 14 cm (5.6 in) in d.b.h. In 20 years the trees will average 22 m (72 ft) and 19 cm (7.5 in); in 40 years, 31 m (101 ft) and 49 cm (19.4 in). The tallest trees are 43 m (140 ft) high; the largest diameters about 122 cm (48 in) *(4)*. Black willows in the North and those on poor sites in the South generally reach a maximum height of 9 to 18 m (30 to 60 ft) and 15 to 46 cm (6 to 18 in) in d.b.h. These seldom furnish a satisfactory saw log.

In well-stocked stands on the best alluvial soils, particularly along the Mississippi River, the tree prunes itself well and produces an acceptably straight trunk which is clear of limbs for an average of 12 m (40 ft). Open-grown willows and willows among small streams and in swamps are generally limby and of limited usefulness. Being a very weak tree, it is especially prone to breakage; almost all large trees have large broken limbs *(4)*.

Unmanaged stands in the South have been estimated to yield 315 m^3/ha (50 cords/acre) at age 25 and 416 m^3 (66 cords) at age 35. The sawtimber volume (Scribner rule) in similar stands has been estimated at 396 m^3/ha (28,300 fbm/acre) at 35 years and 560 m^3/ha (40,000 fbm/acre) at 50 years. Good sites sustain about 30 m^2 of basal area per hectare (130 ft^2/acre) *(4)*.

Black willow is short lived; the greatest age recorded for a sound tree is 70 years and for an unsound tree, 85 years. The average black willow is mature in 55 years *(4)*.

Thinning increases yields and reduces mortality when carried out in relatively young (18 to 24 yr) stands. Growth is best when basal area is reduced by about one-half. Spacing between trees after thinning should average 21 times the mean stem diameter—25.4-cm (10-in) trees spaced 5.3 m (17.5 ft) apart. If the factor is 18 or less, the spacing is probably too dense; if 24 or greater, the site is probably not fully utilized *(2)*.

Rooting Habit—Willow tends to be shallow rooted, especially on clay-capped alluvial soils. It is seldom found on soil types that undergo seasonal dehydration but is more often present on soils with higher water tables throughout the summer months. Floods may deposit more layers of alluvium in established stands. New roots often develop from adventitious buds formed within the previously exposed trunk. By this means, soil is captured and held to form additional land areas along river courses. Willows also sucker readily. Under certain conditions, an essentially pure willow stand of 1 or more hectares (2.5 acres) may consist of relatively few clones.

Reaction to Competition—Black willow is less tolerant of shade than any of its associates and may most accurately be classed as very intolerant. It usually grows in dense, even-aged stands, in which natural mortality is very heavy from sapling stage to maturity. Trees fail to assert dominance, so willow stands periodically stagnate. Stands not properly thinned may lose up to 50 percent of their volume in

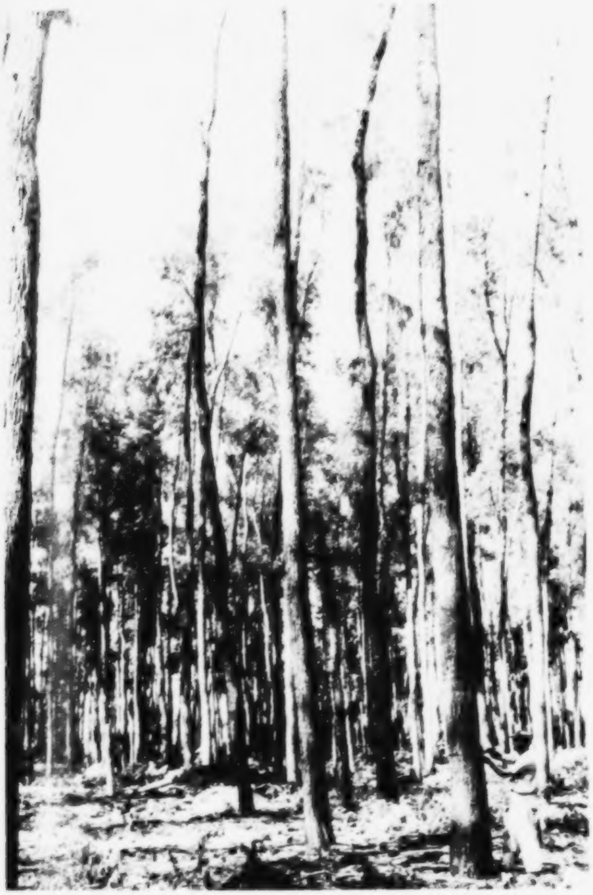

Figure 2—*Twenty-four-year-old black willow stand thinned from basal area of approximately 30 to 17 m²/ha (130 to 75 ft²/acre).*

5 to 8 years *(4)*. Because of its intolerance and the absence of exposed mineral soil under existing stands, willow does not succeed itself naturally unless fresh sediment is deposited as the stand begins to open up. Thinning should remove the understory trees and must be light to prevent the heavy windthrow and stem breakage, which is common in very open stands. Light, early, and frequent thinning forestalls stagnation and mortality *(2)*. An apparently satisfactory thinning prescription is to leave a stand of about 14.9 to 17.2 m²/ha (65 to 75 ft²/acre) of basal area (fig. 2). Heavy epicormic branching may result if weak trees are released.

Damaging Agents—Several insects attack live willow but few cause serious damage. The forest tent caterpillar *(Malacosoma disstria)*, the gypsy moth *(Lymantria dispar)*, the cottonwood leaf beetle *(Chrysomela scripta)*, the willow sawfly *(Nematus ventralis)*, and the imported willow leaf beetle *(Plagiodera versicolora)* sometimes partially, occasionally completely, defoliate willow trees, reducing growth but seldom killing. Stem borers, such as the cottonwood borer *(Plectrodera scalator)* attack willows and may kill by girdling the base. Twig borers, like the willow-branch borer *(Oberea ferruginea)*, feed on the branches and cause deformities that may be undesirable in ornamentals.

Insects are frequently the vectors for disease organisms. Willow blight, the scab and black canker caused by *Pollaccia saliciperda*, is transmitted by borers. Members of the genus *Salix* are the only known hosts. *Phytophthora cactorum* causes bleeding canker, lesions on the lower trunk that discharge a dark-colored, often slimy liquid. Confined to the phloem and cambium area, it can result in death if the canker girdles the trunk. *Cytospora chrysosperma* causes canker in poplar and willow. Under forest conditions, cytospora canker is of little consequence but when trees become weakened by drought, competition, or neglect, losses can be heavy. In nursery beds, losses of up to 75 percent of cuttings have been reported. Leaf rust caused by *Melampsora* spp. is common on seedlings throughout the range of black willow. Mistletoes *(Phoradendron* spp.) damage and deform but seldom kill willows.

The yellow-bellied sapsucker feeds on sap from holes they peck through the bark; this early injury to the tree degrades the lumber sawn later.

Hot fires kill entire stands. Slow, light fires can seriously wound willow, allowing woodrotting fungi to enter. Once dead, willow deteriorates very rapidly. Top and branch rot account for 86 percent of the cull in willow.

Special Uses

The wood is light (specific gravity 0.34 to 0.41), usually straight grained, without characteristic odor or taste, weak in bending, compression, and moderately high in shock resistance. It works well with tools, glues well, and stains and finishes well but is very low in durability.

The wood was once used extensively for artificial limbs, because it is lightweight, doesn't splinter easily, and holds its shape well. It is still used for boxes and crates, furniture core stock, turned pieces, table tops, slack cooperage, wooden novelties, charcoal, and pulp.

Black willow was a favorite for soil stabilization projects in the early efforts at erosion control. The ease with which the species establishes itself from cuttings continues to make it an excellent tree for revetments.

Ancient pharmacopoeia recognized the bark and leaves of willow as useful in the treatment of rheumatism. In 1829, the natural glucoside *salicin* was isolated from willow. Today it is the basic ingredient of aspirin, although salicyclic acid is synthesized rather than extracted from its natural state.

Genetics

Population differences exist but the magnitude and distribution of the variation of specific characters awaits verification through analysis of provenance and progeny tests. Clonal differences in defoliation of black willow by the cottonwood leaf beetle were noted in experimental plots in Mississippi; feeding was also heavier on the male clones *(6)*. In another study, black willows from two natural stands 160 km (100 mi) apart on the lower reaches of the Mississippi River had significantly different fiber lengths *(8)*.

One or more races of black willow are recognized as varieties by some authorities *(3,9)*. Western black willow (*Salix nigra* var. *vallicola* Dudley) of Southwestern United States and adjacent Mexico was renamed as a species, Goodding willow (*S. gooddingii* Ball). Controversy over whether this is a separate species or a varietal species of black willow still goes on. Two other varieties have been named: *S. nigra* var. *altissima* Sarg. of the Texas gulf coast and *S. nigra* var. *lindheimeri* Schneid. of central Texas.

Although the genus *Salix* is widely distributed and many species occupy sympatric ranges, natural hybrids apparently are not common *(3)*. Putative hybrids are difficult to verify since the identity of one parent is often uncertain. The following willows hybridize with *Salix nigra*: *Salix alba* (*S.* × *hankensonii* Dode), *S. amygdaloides* (*S.* × *glatfelteri* Schneid.), *S. bonplandiana*, *S. caroliniana*, *S. lucida* (*S.* × *schneideri* Boivan), and *S. sericea*.

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Sassafras albidum (Nutt.) Nees **Sassafras**

Lauraceae **Laurel family**

Margene M. Griggs

Sassafras *(Sassafras albidum)*, sometimes called white sassafras, is a medium-sized, moderately fast growing, aromatic tree with three distinctive leaf shapes: entire, mittenshaped, and threelobed. Little more than a shrub in the north, sassafras grows largest in the Great Smoky Mountains on moist well-drained sandy loams in open woodlands. It frequently pioneers old fields where it is important to wildlife as a browse plant, often in thickets formed by underground runners from parent trees. The soft, brittle, lightweight wood is of limited commercial value, but oil of sassafras is extracted from root bark for the perfume industry.

Habitat

Native Range

Sassafras (fig. 1) is native from southwestern Maine west to New York, extreme southern Ontario, and central Michigan; southwest in Illinois, extreme southeastern Iowa, Missouri, southeastern Kansas, eastern Oklahoma, and eastern Texas; and east to central Florida *(8)*. It is now extinct in southeastern Wisconsin but is extending its range into northern Illinois *(5)*.

Climate

Average annual rainfall varies from 760 to 1400 mm (30 to 55 in) within the humid range of sassafras. Of this, 640 to 760 mm (25 to 30 in) occur from April to August, the effective growing season. At the northern limits of the range, the average annual snowfall is between 76 to 102 cm (30 to 40 in), while in the southern limits there may be only 2.5 cm (1 in) or less. The average frost-free period is from 160 to 300 days. In January average temperatures are -7° C (20° F) in the north and 13° C (55° F) in the south; the average July temperatures vary from 21° to 27° C (70° to 80° F).

Soils and Topography

Sassafras can be found on virtually all soil types within its range. It grows best in open woods on moist, well-drained, sandy loam soils, but is a pioneer species on abandoned fields, along fence rows, and on dry ridges and upper slopes, especially following fire. In the South Atlantic and Gulf Coast States where sites are predominately sandy soils, mature sassafras seldom exceeds sapling size. On the Lake Michigan dunes of Indiana, it grows on pure, shifting sand *(5)*. It is also found on poor gravelly soils and clay loams. Sassafras is most commonly found growing on soils of the orders Entisols, Alfisols, and Ultisols. Optimum soil pH is 6.0 to 7.0 *(14)*. The species is found at elevations varying from well-drained Mississippi River bottom lands and loessial bluffs to 1220 m (4,000 ft) in the southern Appalachian Mountains *(10,11)*.

Associated Forest Cover

Sassafras is included in only two forest cover types; however, scattered trees of the species are found in many eastern forest types *(13)*. Sassafras–Persimmon (Society of American Foresters Type 64) is a temporary type common on abandoned farmlands throughout the range of sassafras, especially in the lower Midwest and, to a limited extent, the mid-Atlantic States. It is also present as successional stands on old fields in the Southeastern States where pine usually predominates. Sassafras is a minor component in Bear Oak (Type 43), a scrub type appearing on dry sites along the Coastal Plain from New England southward to New Jersey, and from northwestern New Jersey southward to scattered localities in western Virginia and eastern West Virginia. It is also prevalent in eastern and central Pennsylvania.

Additional common associated tree species are sweetgum *(Liquidambar styraciflua)*, flowering dogwood *(Cornus florida)*, elms *(Ulmus* spp.), eastern redcedar *(Juniperus virginiana)*, hickories *(Carya* spp.), and American beech *(Fagus grandifolia)*. In fields with deeper soils it grows with elms, ashes *(Fraxinus* spp.), sugar maple *(Acer saccharum)*, yellow-poplar *(Liriodendron tulipifera)*, and oaks *(Quercus* spp.).

Noteworthy minor tree associates are American hornbeam *(Carpinus caroliniana)*, eastern hophornbeam *(Ostrya virginiana)*, and pawpaw *(Asimina triloba)*. On poorer sites, particularly in the Appalachian Mountains, it is frequently associated with black locust *(Robinia pseudoacacia)*, red maple *(Acer rubrum)*, sourwood *(Oxydendrum arboreum)*, and several oaks. At the northern edge of its range, sas-

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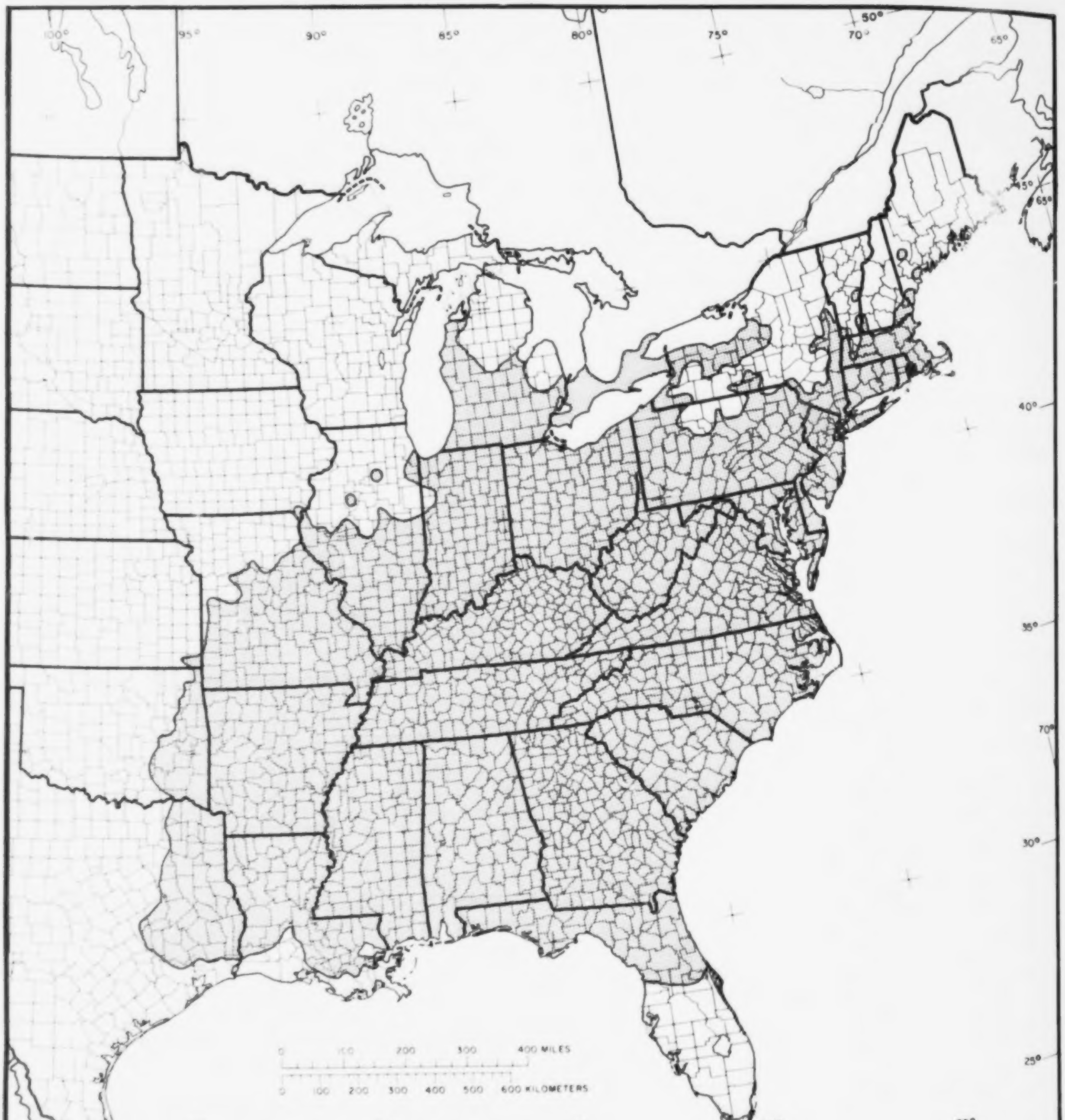
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Figure 1—*The native range of sassafras.*

safras is found in the understory of aspen (*Populus* spp.) and northern pin oak (*Quercus ellipsoidalis*) stands (*8*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sassafras is dioecious. Greenish-yellow flowers appear in March and April as the leaves unfold. They develop in loose, drooping few-flowered axillary racemes.

The fruit, 8 to 13 mm (0.3 to 0.5 in) long, is a single-seeded dark-blue drupe. It matures in August and September of the first year. The fruit is borne on a thickened red pedicel, and the pulpy flesh covers the seed.

Seed Production and Dissemination—Seed production begins when trees approach 10 years of age and is greatest when trees are 25 to 50 years old. Good seed crops are produced every 1 or 2 years (*2*). There are 8,800 to 13,200 seeds/kg (4,000 to 6,000/lb) and soundness is 35 percent. Birds are principal agents of seed dissemination, with water a secondary agent. Some seeds probably are distributed by small mammals.

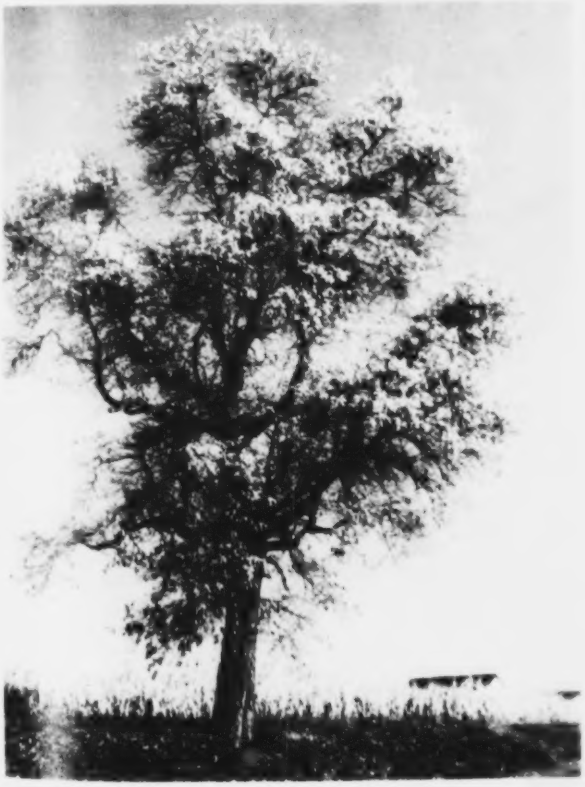

Figure 2—*Sassafras tree in Mississippi.*

Seedling Development—Sassafras seed usually remains dormant until spring, although some early maturing seed may germinate in fall. The limit for storage of sassafras in the forest floor is about 6 years (*15*). Stratification for 120 days in moist sand at 5° C (41° F) breaks natural dormancy (*2*). The best seedbed is a moist, rich, loamy soil with a protective cover of leaves and litter. Germination is hypogeal.

Sassafras is intolerant of shade and reproduction is sparse and erratic in wooded areas. Subsequent reproduction is usually vegetative. The dense thickets often found in woods openings or in old fields develop from root sprouts rather than seed. On good sites where competition is not heavy, the sprouts may grow 3.7 m (12 ft) in 3 years and sometimes are abundant (*3*). Elsewhere growth is slow. Because sassafras grows in dense stands and sprouts prolifically, it is a difficult cover type to convert to pine or more desirable hardwoods.

Vegetative Reproduction—Sassafras reproduces easily by root sprouts. In parts of its ranges, sprouts rapidly restock abandoned farmlands (*3*). Sprouting is prolific from the stumps of young trees. Sassafras can be propagated fairly well from root cuttings, but not from stem cuttings. Two cutting types—roots with a stem sprout planted vertically and large roots planted horizontally—were found to be superior (*9*).

Sapling and Pole Stages to Maturity

Growth and Yield—Sassafras varies in size from shrubs to large trees with straight, clear trunks. The short, stout branches spread at right angles to form a narrow flat-topped crown (fig. 2). It may attain heights of 30 m (98 ft) on the best sites. On poor sites, especially in the northern part of its range and in Florida, sassafras is short and shrubby (*12*). Mature trees may average only 15 to 20 cm (6 to 8 in) in d.b.h., with a maximum of about 38 cm (15 in). Natural pruning is good in well-stocked stands.

Rooting Habit—Sassafras roots are shallow and of the prominent lateral type. The long laterals extend for a distance with little change in diameter, branch occasionally, and form an increasingly complex system (*3*). The laterals are practically all from 15 to 50 cm (6 to 20 in) deep, rising and falling at various intervals. Lateral spread is at the rate of 74 cm (29 in) per year. The forming of a sucker results in the development of feeding roots that otherwise would not be present on the lateral. These roots arise near the sucker and on the larger part of the lateral. They branch to very fine rootlets that are quite important in the species adaptability to vigorous growth on various types of soil.

Reaction to Competition—Sassafras is classed as intolerant of shade at all ages. In forest stands, it usually appears as individual trees or in small groups and is usually in the dominant overstory. In the understory along the edges of heavy stands it may live, but generally does not reach merchantable size. If it becomes overtopped in mixed stands, it is one of the first species to die. Allelopathy seems to be the mechanism that allows sassafras, when it has invaded abandoned fields, to maintain itself aggressively in a relatively pure and mature forest *(4)*. Field studies revealed that 10 species consistently appear exclusively outside of clump canopies of sassafras, and 7 other species predominated beneath the sassafras canopy. Annual herbs were effectively excluded from the understory flora. The allelopaths produced by sassafras are believed to be 2-pinene, 3-phellandrene, eugenol, safrole, citrol, and s-camphor *(4)*.

Damaging Agents—Sassafras is highly susceptible to fire damage at any age. Light fires kill reproduction and small saplings, and heavier burns injure large trees and provide entry for pathogens. Sassafras may die if not well protected from extremes of winter weather.

Foliage diseases are primarily the main damaging agents to sassafras. *Actinopelte dryina* is largely a southern fungus severely blighting the leaves. *Mycosphaerella sassafras* is one of the most widely occurring leaf spots of sassafras. A *Nectria* canker on trunks is fairly common in the southern Appalachian region. Remarkably, few reports of wood-rot fungi on sassafras have appeared in the literature *(6)*. Mistletoe *(Phoradendron flavescens)* has been reported *(8)*.

At least 15 species of insects attack sassafras, including root borers, leaf feeders, and sucking insects. Except for small local outbreaks, damage is relatively unimportant. From New York to Florida, the larvae of a wood-boring weevil *(Apteromechus ferratus)* kills trees up to 25 cm (10 in) in diameter. Two leaf feeders, the gypsy moth *(Lymantria dispar)* and looper *(Epimecis hortaria)*, are found on sassafras in the Northeastern United States and in the Atlantic States, respectively. Sassafras is probably one of the favorite forest tree foods of the Japanese beetle *(Popillia japonica) (8)*.

Special Uses

The bark, twigs, and leaves of sassafras are important foods for wildlife in some areas. Deer browse the twigs in the winter and the leaves and succulent growth during spring and summer. Palatability, although quite variable, is considered good throughout the range. In addition to its value to wildlife, sassafras provides wood and bark for a variety of commercial and domestic uses. Tea is brewed from the bark of roots. The leaves are used in thickening soups. The orange wood has been used for cooperage, buckets, posts, and furniture *(7)*. The oil is used to perfume some soaps. Finally, sassafras is considered a good choice for restoring depleted soils in old fields. It was superior to black locust or pines for this purpose in Indiana and Illinois *(1)*.

Genetics

No genetic variation has been reported for sassafras.

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Tabebuia heterophylla (DC.) Britton

Roble Blanco, White-Cedar

Bignoniaceae Bignonia family

P. L. Weaver

Roble blanco or white-cedar *(Tabebuia heterophylla)* is a small- to medium-size, mostly deciduous tree with showy pink flowers. It grows on any soil type and will adapt to poor or degraded soils if moisture is available. Valued as a timber tree, it has been widely planted for both reforestation and ornamentation. The tough strong wood is used for many products and is favored for boat building in the Lesser Antilles.

Habitat

Native Range

Roble is native to Puerto Rico and widely distributed through the West Indies from Hispaniola to Grenada and Barbados. It is also naturalized in Bermuda and planted in southern Florida *(16)*.

In Puerto Rico, it is widespread in abandoned pastures and secondary forests and found in dry or wet natural forests, except for the highest elevations in the Luquillo Mountains and the Cordillera Central. Elsewhere in the Caribbean, roble is particularly common in dry, coastal woodlands and in secondary forests.

Climate

In Puerto Rico, roble is found principally in the Subtropical Dry, Subtropical Moist, and Subtropical Wet life zones *(12,15)* where the annual rainfall varies from about 850 to 2500 mm (33 to 98 in). Temperature ranges from a mean minimum in January of 16° C (61° F) to a mean maximum of 31° C (88° F) in August *(5)*. Potential evapotranspiration over the same regions varies between 1400 and 1900 mm (55 and 75 in) annually, with the lowest measurements in the mountainous interior.

Throughout the West Indies, roble is found predominately in areas where the annual rainfall varies between about 1000 and 2500 mm (39 and 98 in) (table 1). All sites are frost free.

Table 1—Presence of roble blanco *(Tabebuia heterophylla)* in tropical forests of the Western Hemisphere

Islands	Forest types[1]
Puerto Rico	Dry Evergreen Forest Lower Montane Rain Forest
Nevis	Dry Evergreen Forest
St. Kitts	Dry Evergreen Forest
Dominica	Dry Scrub Woodlands Fire grassland and standards
St. Lucia	Littoral Woodland Dry Scrub Woodlands Secondary Woodlands
St. Vincent	Dry Scrub Woodlands
Grenadines	Dry Scrub Woodlands
Grenada	Dry Scrub Woodlands
Antigua	Secondary Woodlands
Barbuda	Bush land
Anguilla	Bush land
Barbados	Dry Scrub Woodlands
Martinique	Seasonal Forests Dry Scrub Woodlands
Guadeloupe	Dry Scrub Woodlands Littoral Woodland
British Virgin Islands	Dry Scrub Woodland Xerophytic Rain Forest

[1] Roble is found throughout the Windward and Leeward Islands as a component of the Dry Zone Flora with rainfall between 900 to 1700 mm/yr (35 to 65 in/yr). In all instances classification is according to Beard *(1,2,3)*.

Soils and Topography

In Puerto Rico, roble is found on sand, limestone, and heavy clay soils, acid or alkaline in reaction, and residual, alluvial, or colluvial in origin. It appears to grow best, however, on deep clays. Roble is a cosmopolitan species and is found on all soils presently identified in Puerto Rico. The most common soil order on the island is Inceptisols. Physiographically, it is most common on slopes and ridges *(19)* but is also found on flats adjacent to river beds *(9)*. In general, it is tolerant of degraded sites and abandoned farm lands where it tends to form nearly pure stands.

In Puerto Rico, roble is planted on poor sites to provide cover and to improve the soil. It is recommended for planting on uniform and convex slopes and ridges, where trials have shown it to be a

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promising species for reforestation *(20)*. It has also done well on humid, waterlogged sites.

Associated Forest Cover

In Puerto Rico, roble is associated with algarrobo *(Hymenaea courbaril)*, laurel avispillo *(Nectandra coriacea)*, guamá *(Inga fagifolia)*, and laurel geo *(Ocotea leucoxylon)* in the Dry Evergreen Forest (classification according to Beard, *1,2,3*). In the Lower Montane Rain Forest of the Luquillo Mountains it is found associated with guamá, yagrumo macho *(Didymopanax morototoni)*, palo de matos *(Ormosia krugii)*, achiotillo *(Alchornea latifolia)* and various composites, all of which are constituents of the secondary vegetation *(9)*.

In the Windward and Leeward Islands, roble is frequently found with the same species listed for the Dry Evergreen Forest of Puerto Rico. Beard *(2)* called this the dry zone flora, of which the Dry Evergreen Forests, Dry Scrub Woodland, and Littoral Woodland are the principal forest types.

Life History

The mature roble in Puerto Rico is easily identified by its opposite, palmately compound leaves, furrowed bark, and narrow, columnar crown (fig. 1). It is a small- to medium-size tree attaining a height of 18 m (60 ft) and a diameter of 60 cm (25 in). In the seedling and sapling stages, roble is an aggressive pioneer.

Reproduction and Early Growth

Flowering and Fruiting—Large white to light purple perfect flowers are borne few to several in terminal and lateral clusters, or occasionally as individuals. In Puerto Rico, flowering is chiefly in the spring, or dry season, and is accompanied by complete leaf drop *(11,16)*. Sporadic flowering occurs at other times. Fruits are borne in May and June with fruit fall varying from July through September. Mature fruits, dark brown cigarlike pods, may be found on the tree during most of the year *(16)*.

At 55 randomly placed collection stations comprised of 0.5 m^2 (5.4 ft^2) screen baskets in the Subtropical Wet Forest of Puerto Rico, roble dropped 39 fruits in 39 months. Of the 38 species observed, roble ranked 37th in the number of fruits collected *(11)*.

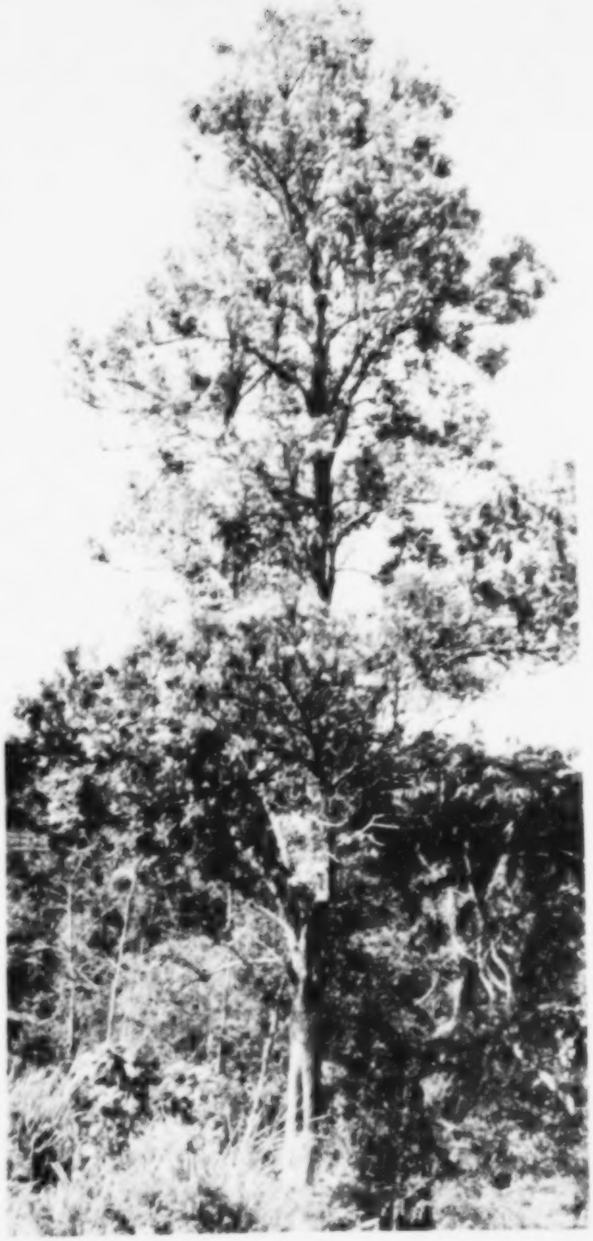

Figure 1—*Roble, showing narrow, columnar crown, characteristic even of open-grown trees.*

Seed Production and Dissemination—The fruits are pods, about 8 to 20 cm (3 to 8 in) long and 6.5 mm (0.25 in) in diameter. The pods contain many winged seeds each about 2 cm (0.79 in) long. The capsule splits along two lines and seeds are dispersed varying distances from the parent tree, ranging up to 100 m (330 ft) or more, depending upon weather conditions. Dispersal is by wind. The seeds germinate in open areas and form dense stands of seedlings.

Several seed experiments were conducted at the Institute of Tropical Forestry during the mid-1940's. About 70,000 air-dried seeds were counted per kilogram (31,750/lb), and these had a mean moisture content of 31 percent, based on the dry weight of the seeds. Seeds sown directly in seedbeds after collection in the field showed germination rates of 90 percent within 2 weeks. A 3-week delay in sowing seeds reduced viability to about 55 percent and after 5 weeks, no seeds germinated. Attempts were made to store seeds for long periods using seed moisture contents of 100, 75, 50, and 25 percent at room temperature and at 4° C (40° F). The best germination after 25 months, nearly 55 percent, was attained with the lowest moisture content and temperature combination.

Seedling Development—Germination of roble is epigeal. Experiments by staff of the Institute of Tropical Forestry established roble in two different regions by means of broadcast seeding, spot planting of seeds, and planting, on lands that had been burned, cleared in a swath 1 m (3.3 ft) wide, or planted without site treatment. Direct seeding proved unsuccessful. The nursery stock survived, although the seedlings suffered dieback and did not recover for 6 to 8 months. Site treatment did not influence survival because grass grew quickly on all areas under study and competed with the transplants. The seedlings, after recovery, grew slowly.

Transplanting of wildlings was found preferable to nursery stock because they are abundant and have better root systems *(21)*. In some instances, however, dieback of the leader was observed. Pruned wildlings and shelterwood plantings of wildlings were then tested, but neither gave better results. Survival remained good, but growth was not improved.

The lesson learned from testing of roble wildlings was that survival is high, even on waterlogged soils and exposed ridges. Leaves are lost after transplanting and the wildlings require about 6 to 8 months to recover, if rainfall is adequate. Of the size classes tested ranging through 60 cm (24 in), the best results were attained with the largest wildlings. Subsequent growth in all instances was slow and averaged about 1.8 m (6 ft) in 2 years.

Vegetative Reproduction—Cuttings were tested on degraded heavy soils in Luquillo Forest and Carite, but only a few survived *(19,20)*. Roble fence posts have been observed to sprout *(26)*, but vegetative reproduction cannot be relied on for reforestation.

Sapling and Pole Stages to Maturity

Growth and Yield—Roble regenerates well in open fields and develops into a dense stand of seedlings, after which it appears to stagnate. This phenomenon may be partially attributable to the shallow, infertile soils and to exposure. The density of the seedling stands may also be a contributing factor.

Plantations established in Puerto Rico show that the dominant and codominant stems averaged about 1 m (3.3 ft) in height growth and 1 cm (0.4 in) in diameter growth annually over a period of 11 to 14 years (table 2). Annual basal area growth was about 1.5 m²/ha (6.5 ft²/acre). Height growth in Hawaii was less, but the measurements were for smaller trees over a shorter period of time.

Within natural forest, diameter increment varies between 0.28 to 0.39 cm (0.11 to 0.15 in) annually for all sites with the exception of limestone ridges where growth was only 0.13 cm (0.05 in) (table 2). In a study of several crop trees within the Sabana compartment of the Luquillo Forest, roble was found to grow significantly slower than the remaining species *(10)*. Differences by crown class were evident. On more than 435 trees within the Sabana 8 compartment, annual diameter growth for dominants was 0.38 cm (0.15 in), codominants 0.32 cm (0.13 in), intermediates 0.21 cm (0.08 in), and suppressed stems 0.09 cm (0.03 in). Moreover, diameter growth increased with increasing diameter class, perhaps due to a more favorable competitive position within the canopy *(10)*.

From a sample of 360 trees ranging in diameter from 9 to 40 cm (3.5 to 15.7 in) growing within a secondary, thinned stand, it was estimated that roble would attain the 40 cm (16 in) diameter class in about 100 years.

Rooting Habit—The use of wildlings as planting stock revealed that young roble develops a thick stem and well-developed root system at an early age *(21)*.

Reaction to Competition—The silviculture of roble was also investigated by the staff of the Institute during the mid-1940's. Roble wildlings underplanted in an Australian beefwood *(Casuarina equisetifolia)* stand, a species used to provide a light shade, showed 80 percent survival after 18 months, but growth was very slow. In another experiment with nursery seedlings raised in sun vs. shade conditions, 40 percent greater height growth was ob-

Table 2—Growth information for roble blanco (*Tabebuia heterophylla*) in the Western Hemisphere

	Site characteristics			Stand		Mean annual increment		
Location	Elevation	Annual rainfall	Soil	Age[1]	Density	Height	D.b.h.	Basal area
	m	*mm*		*yr*	*stems/ha*	*m*	*cm*	*m²/ha*
Plantations								
Puerto Rico								
Luquillo[2] *(25)*	300	3050	residual clay	11	NA[3]	1.3	1.18	1.82
Luquillo[2] *(25)*	250	2550	residual clay	14	1000	1.0	0.93	1.29
Luquillo *(19)*	360	2700	eroded ridge	5	400	0.5	0.71	0.32
Hawaii *(28)*	30 to 625	2250 to 5600	stoney muck	5.3	NA	0.6 to 0.7	NA	NA
Hawaii *(28)*	180	700	stoney clay	5.6	NA	0.3	NA	NA
Natural forest								
Puerto Rico								
Sabana *(10)*	180 to 360	2300	deep acid clay	17	NA	NA	0.28	NA
Rio Grande *(10)*	420 to 600	3300	deep acid clay	17	NA	NA	0.35	NA
Cubuy	300 to 550	2000	clay loam	17	NA	NA	0.30	NA
St. Just *(27)*	60	1900	shallow clay	2	2150	NA	0.38	NA
Cambalache *(27)*	60	1400	limestone ridge	25	4350	NA	0.13	NA
El Verde *(24)*	450	3000	acid clay	2	NA	NA	0.38	NA
Luquillo Foothills *(24)*	200	2500	acid clay	11	2420	NA	0.39	NA
Luquillo Foothills *(24)*	200	2500	acid clay	11	2700	NA	0.28	NA
	ft	*in*		*yr*	*stems/acre*	*ft*	*in*	*ft²/acre*
Plantations								
Puerto Rico								
Luquillo[2]	984	120	residual clay	11	NA	4.26	0.46	7.93
Luquillo[2]	820	100	residual clay	14	405	3.28	0.37	5.62
Luquillo	1,130	106	eroded ridge	5	162	1.64	0.28	1.40
Hawaii	98 to 623	98 to 220	stoney muck	5.3	NA	1.97 to 2.30	NA	NA
Hawaii	590	28	stoney clay	5.6	NA	0.98	NA	NA
Natural forest								
Puerto Rico								
Sabana	590 to 1,180	90	deep acid clay	17	NA	NA	0.11	NA
Rio Grande	1,378 to 1,968	130	deep acid clay	17	NA	NA	0.14	NA
Cubuy	984 to 1,804	78	clay loam	17	NA	NA	0.12	NA
St. Just	197	75	shallow clay	2	870	NA	0.15	NA
Cambalache	197	55	limestone ridge	25	1,760	NA	0.05	NA
El Verde	1,476	118	acid clay	2	NA	NA	0.15	NA
Luquillo Foothills	256	98	acid clay	11	1,093	NA	0.15	NA
Luquillo Foothills	256	98	acid clay	11	1,093	NA	0.11	NA

[1] As used in natural forests, age refers to the duration of measurements.

[2] Growth increment recorded for dominant and codominant stems.

[3] Not available.

served in the exposed conditions after 5 months. Shaded seedlings grew very little. In natural conditions, wildlings are capable of surviving shade for years with no appreciable growth *(21)*.

Roble regenerates and forms pure stands on grasslands and degraded soils, in particular on exposed upper slopes and ridges, where competition from faster growing, larger, and more tolerant trees is lacking *(19)*. Plantations of roble wildlings usually require weedings where grass is dense, one at 6 months and a second at about 18 months. Plantations should have close spacing, not greater than 1.8 by 1.8 m (6 by 6 ft), so that ground cover is provided rapidly *(21)*.

Within the Lower Montane Rain Forest *(1,2,3)* of the Luquillo Mountains, roble was found on four of six permanent plots totaling 2.1 ha (5.2 acres), measured since the mid-1940's. Of the 30 species studied, it ranked 25th in density, 14th in basal area dominance, and 15th in volume *(4)*. Moreover, on a scale of 1 (most tolerant) to 29 (most pioneer), roble ranked 20th in shade tolerance among tree species in the Luquillo Forest *(23)*. The scale considered the presence of seed, seedlings, and understory trees within the forest. Overall, roble blanco is classed as intolerant of shade.

Roble's persistence in the natural forest, despite its slow growth, is largely attributable to its capacity to survive on poor sites where competition is minimized.

Damaging Agents—In the natural forest, pathogens do not appear to be of any consequence. However, branches of city and roadside trees are often deformed into a witches' broom appearance, apparently by a virus possibly transmitted by the leaf hopper *Protalebra tabebuiae* (*8*). The insect also defoliates the tree or causes the leaves to turn yellow and fall prematurely (*16,22*). A similar disease on a closely related species *Tabebuia pentaphylla*, was observed on trees grown for cacao shade on the Paria peninsula of Venezuela (*7*). Because of the numerous problems with pathogens, some authorities have recommended that closely related members of the same genus be used as substitutes in ornamental plantings.

A dieback disease was observed in 3 percent of potted trees in the Cambalache nursery on the north coast of Puerto Rico and was attributed to *Botryodiplodia* spp. (*13*). Transplants from a nearby wooded area to a golf course near the town of Dorado were infested by a shoot borer, probably *Pachymorphus subductellus* (*14*).

The heartwood is rated as moderately durable in contact with the ground, but susceptible to *Cryptotermes brevis*, the dry wood termite (*6,29*) and marine borers (*16*). Moreover, the wood rates only fair in weathering characteristics. Unpainted wood loses its smooth surface and develops considerable checking (*17*).

Special Uses

The heartwood is light brown or golden and not easily separated from the sapwood. The grain is straight to interlocked, and the specific gravity is about 0.55. The wood seasons rapidly with little warping and is fairly easy to work, rating fair for planing, excellent for boring, mortising, and sanding, and good for turning. Penetration and absorption of preservatives is low, even in the sapwood (*6,16,17,18*). The wood is tough and strong for its weight.

Roble's appearance and technical properties resemble both oak and ash. The wood is widely used for flooring, furniture, cabinetwork, interior trim, tool handles, decorative veneers, boatbuilding, ox yokes, millwork, and sporting goods. Less valuable grades are suitable for boxes, crates, concrete forms and similar items, and occasionally for posts and poles (*16,17,18*).

Roble's large flowers and narrow, columnar crown have made it a favorite ornamental in yards and along roadsides throughout Puerto Rico. Flowering in many instances has been observed a few years after planting (*22*).

The tree comes in readily on abandoned farm soils and is particularly adapted to degraded sites. Foresters have planted it on abandoned farmlands where its growth has been slow, but satisfactory.

Roble is also classed as a honey plant.

Genetics

Tabebuia heterophylla is a variable species that has been classified into subspecies, or related species, by several authors. Synonyms considered by some as varieties include *T. pallida* (Lindl.) Miers and *T. dominguensis* Urban (*18*).

Roble in Puerto Rico typically has five leaflets. In dry areas and coastal thickets in the Lesser Antilles, trees are shorter, fruits and seeds smaller, and leaflet number declines to three, or at times to a single leaflet. Another variation found in Guadeloupe, Dominica, and Martinique has a single, broadly elliptic leaf (*16*).

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Tilia americana L. American Basswood

Tiliaceae Basswood family

T. R. Crow

American basswood *(Tilia americana)*, northernmost *Tilia* species, is a large, rapid-growing tree of eastern and central hardwood woodlands. Best growth is in the central part of the range on deep, moist soils; development is vigorous from sprouts as well as seed. American basswood is an important timber tree, especially in the Great Lakes States. The soft, light wood has many uses in wood products. The tree is also well known as a honey-tree, and the seeds and twigs are eaten by wildlife. It is commonly planted as a shade tree in urban areas of the eastern states where it is called American linden.

Habitat

Native Range

American basswood (fig. 1) ranges from southwestern New Brunswick and New England west in Quebec and Ontario to the southeast corner of Manitoba; south through eastern North Dakota, South Dakota, Nebraska, and Kansas to northeastern Oklahoma; east to northern Arkansas, Tennessee, western North Carolina; and northeast to New Jersey.

Climate

Climatic conditions associated with the species range are generally continental—cold winters, warm summers, and a humid to subhumid moisture regime. Mean annual precipitation within the species range is 530 mm (21 in) at the western limit and 1140 mm (45 in) in the northeast. The northern limit of basswood approximates the -18° to -17° C (0° to 2° F) isotherm for mean daily minimum January temperature. Basswood reaches its maximum development in areas averaging 18° to 27° C (65° to 80° F) in July and receiving 250 to 380 mm (10 to 15 in) of precipitation during the growing season. The frost-free growing period varies from 80 to 180 days within its range.

Soils and Topography

Studies relating to the presence of basswood to soil characteristics in Minnesota, Wisconsin, and Michigan indicate that stands in which basswood shared dominance were generally confined to sandy loams, loams, or silt loams, with basswood obtaining maximum development on the finer textured soils. Most soils were classified as Hapludalfs within the Alfisols order, although some Eutrochrepts (Inceptisols), Cryandepts (Inceptisols), mesic families of entic Fragiorthods (Spodosols), and Haplorthods (Spodosols) were noted.

Basswood grows best on mesic sites, but it is also found on coarse soils such as the sand dunes near Lake Michigan *(17)* and on dry, exposed rock ridges in Ontario and Quebec *(25)*.

The species grows on soils ranging in pH from 4.5 to 7.5 but occurs more often in the less acidic to slightly basic part of this range. In fact, calcareous soils have been associated with the presence of basswood *(9,17)*.

The importance of aspect and edaphic factors to local distribution is reflected by the restriction of basswood throughout much of its range to moist sites on north- and east-facing slopes. Maple–basswood forests in southern Wisconsin are largely restricted to northerly exposures *(19)*. Basswood is restricted to more mesic sites in southern Illinois and in northern Kentucky *(5)*. At the western limit of its range, basswood frequently grows on the eastern side of lakes and along major drainages. This localized growth is often ascribed to fire protection. Although lack of fire may be a reason for the persistence of a fire-sensitive species such as basswood, presence and distribution are controlled more by soil moisture and the ameliorating effects of water on the local climate.

Basswood is classified as a nitrogen-demanding species because it grows poorly on sites deficient in nitrogen. With increasing nitrogen supplies, basswood growth increases markedly, approaching a maximum radial increment when 560 to 670 kg/ha (500 to 600 lb/acre) of nitrogen are added. Basswood leaves have high contents of nitrogen, calcium, magnesium, and potassium at the time of leaf fall and they contribute most of these nutrients to the forest floor *(13,28)*.

Associated Forest Cover

American basswood (fig. 2) grows in mixture with other species and only rarely forms pure stands. It is dominant in a single forest type, Sugar Maple—Basswood (Society of American Foresters Type 26). This cover type is most common in central Minnesota

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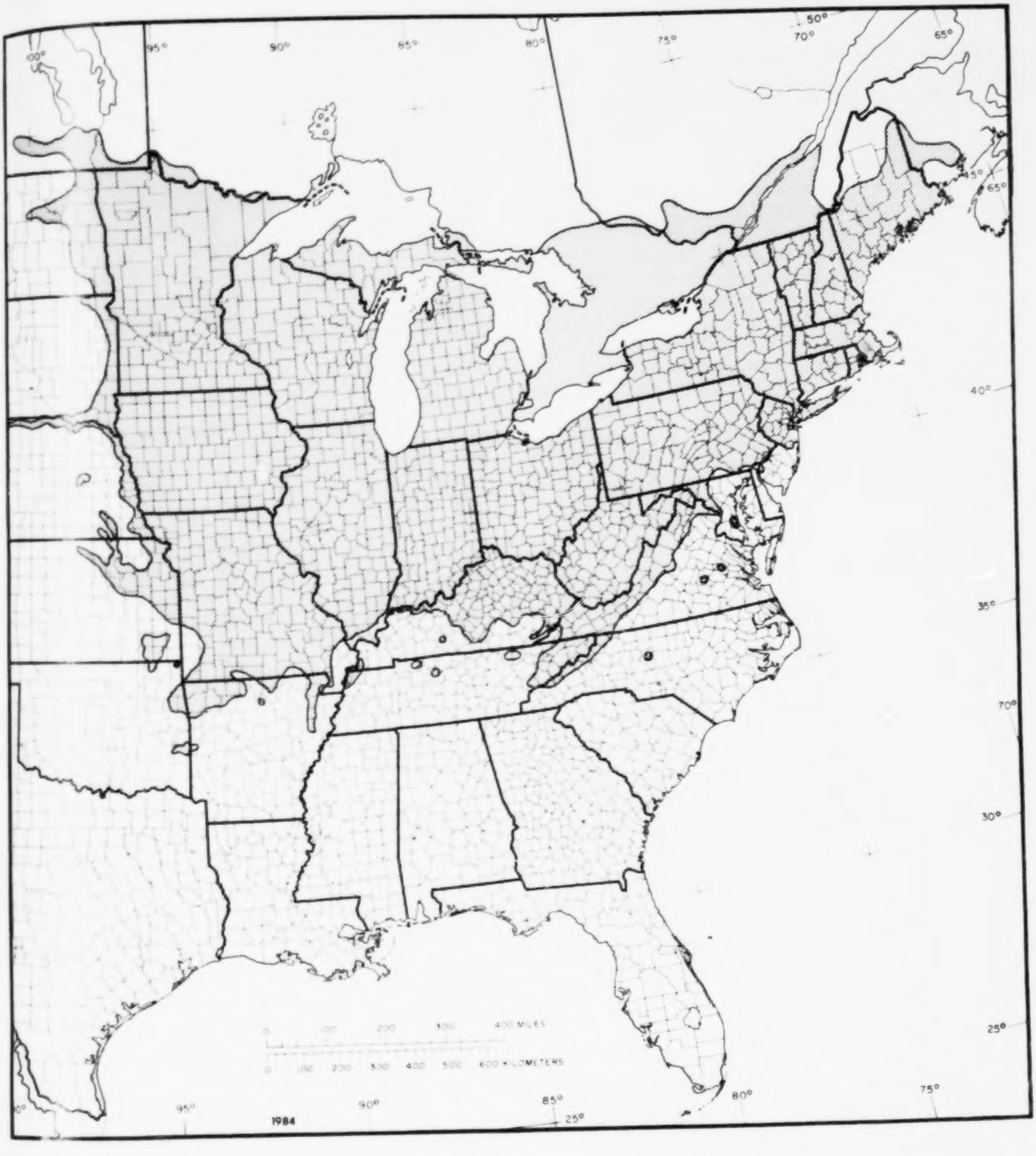
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Figure 1—*The native range of American basswood.*

and western Wisconsin but is represented elsewhere from central Illinois, northward to southern Ontario and Quebec, eastward to northwestern Ohio, and westward along valley slopes of the prairie-forest transition *(15)*.

Sugar maple *(Acer saccharum)* dominates both overstory and understory layers, with basswood achieving the position of second dominant in the tree layer. Common associates are white ash *(Fraxinus americana)*, northern red oak *(Quercus rubra)*, eastern hophornbeam *(Ostrya virginiana)*, red maple *(Acer rubrum)*, and American elm *(Ulmus americana)*.

Although not a dominant species, basswood is also found in the following forest cover types:

21	Eastern White Pine
23	Eastern Hemlock
20	White Pine–Northern Red Oak–Red Maple
24	Hemlock–Yellow Birch
27	Sugar Maple
25	Sugar Maple–Beech–Yellow Birch
28	Black Cherry–Maple
60	Beech–Sugar Maple
39	Black Ash–American Elm–Red Maple
42	Bur Oak
58	Yellow-Poplar–Eastern Hemlock
62	Silver Maple–American Elm

Basswood is one of the major species, with sugar maple, beech *(Fagus)*, ash *(Fraxinus)*, hickory *(Carya)*, and oak *(Quercus)*, in the Deciduous Forest Region of southern Ontario. It is a minor component of the sugar maple–yellow birch–hemlock–white pine climax forest type in the southern districts of the Great Lakes–St. Lawrence regions of Ontario *(32)*.

In the Mixed Mesophytic forests of the southern Appalachians, *Tilia americana* is replaced by *T. heterophylla (9)*. The genotypic distinction between these species is not always clear, and *T. americana* does appear in the northern part of the Mixed Mesophytic region.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The fragrant, yellow-white, perfect flowers are borne on loose cymes on long stalks attached to leafy bracts. Flowering generally occurs in June but can begin in late May or early July, depending on latitude and annual variations in temperature. Flowering follows initial leaf-out and lasts approximately 2 weeks. During this period, all stages of floral development are present on a single tree or even in a single inflorescence (4 to 40 flowers per inflorescence). The flowers attract a number of insect pollinators. In a study of the pollination biology, 66 species of insects from 29 families were identified as pollinators of *Tilia* flowers. Bees and flies were the most common diurnal pollinators; moths were the primary nocturnal visitors *(2)*.

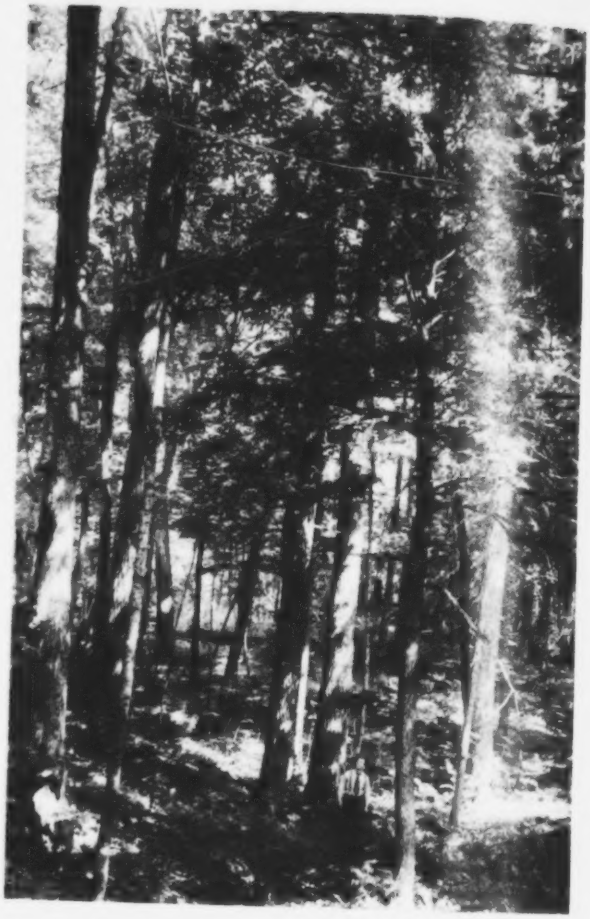

Figure 2—*Stand of virgin mixed hardwoods in Nicolet National Forest, WI. All large trees are basswood. Conifers are hemlock.*

The fruit, a nutlike drupe 5 to 10 mm (0.2 to 0.4 in) in diameter, usually contains one seed but in collections from both open- and forest-grown trees, 12 percent of the fruit contained two seeds and less than 1 percent contained three seeds. The seeds have a crustaceous seed coat (testa), a fleshy yellowish endosperm, and a well-developed embryo. A variety of forms of fruit and seed have been noted, including egg-shaped, round, onion-shaped, conical, and pentagonal *(34)*. Individual trees tend to consistently produce fruit of a particular form and size.

Seed Production and Dissemination—Fruits ripen in September and October and are soon dispersed by such mechanisms as wind, gravity, and animals. Although the flower bracts are reported to aid in wind dispersal, fruits rarely are carried more than one or two tree lengths from the parent *(24)*. In addition to their limited role in seed dispersal, bracts may act as "flags" to attract pollinators (especially nocturnal ones) to the inflorescences *(2)*. Animals probably increase the seed dispersal significantly.

The seed-bearing age for basswood generally ranges from 15 to 100 years, but seed production at age 8 years (10 years from seed) has been noted *(45)*. The number of ripened fruits averages 9,700 to 13,200/kg (4,400 to 6,000/lb); green fruit averages 5,070 to 5,950 seeds per kilogram (2,300 to 2,700/lb) of fruit *(17,33,45)*. Based on a number of collections, seed weights varied from 12 to 38 mg (0.18 to 0.59 gr) and averaged 31 mg (0.48 gr) *(4)*. In a study for 26 years of 19 species in northern Wisconsin, basswood was one of the most consistent fall-maturing seed producers *(18)*. It produced good seed crops 62 percent of the time from 1949 to 1974. When crown-released, basswood that were about 50 years old did not increase their fruit production during the 5-year period following release. Moreover, the quality of fruit remained poor throughout this period. In the third year after release, for example, only 5 percent of the fruit collected from the ground contained sound seed *(37)*.

The production of fruit without seed (parthenocarpy) and seed infestation by a lepidopterous larva are two common defects that affect seed viability. A pin hole in the pericarp indicates the presence of the larvae. The percentage of fruits with the pin hole was 3 percent in a September collection and 7 percent for an October collection in southeastern Ontario *(35)*; 30 percent of fruits were insect infested in 45 collections from various parts of the natural range of basswood *(4)*. In the same collections, the percentage of fruits with seed ranged from 0 to nearly 100, but the lack of sound seed on the forest floor seems to be the rule. Only 2 percent were sound out of more than 7,400 identifiable basswood seeds found in the litter in a northern Wisconsin stand. Seeds covered by leaves had rotted and most of the seeds lying on or in the upper litter layers had been destroyed by rodents *(18)*.

Seedling Development—Basswood seeds show a pronounced dormancy and generally germinate poorly regardless of seedbed conditions. The primary cause for the lack of quick germination is an impermeable testa. Using organic acids to digest the pericarps of the fruits and to render the testas permeable improves germination *(17)*. Correctly treated seeds commonly average from 20 to 30 percent germination following stratification at 2° to 5° C (36° to 41° F) for 110 to 130 days. Germination is epigeal. Early harvesting followed by immediate sowing has also been suggested for overcoming dormancy of basswood seeds. Collections should be made when seed coats turn brown but before they become dry and hard, or more specifically, when the moisture content is 20 to 40 percent of the green weight *(7,29)*.

Shading aids the establishment and initial survival of basswood seedlings but heavy shade limits subsequent growth and development, and vigorous growth is unlikely under the forest canopy. Likewise, higher soil temperatures found in forest openings are suitable for greatest growth of basswood seedlings *(3)*.

Basswood seedlings first develop a long taproot, which is soon supplemented by lateral roots. First-year seedlings had a root penetration of 20.3 cm (8 in) with a lateral spread of 7.6 cm (3 in), and second-year seedlings had a root penetration of 21.3 cm (8.4 in) and a lateral spread of 18.3 cm (7.2 in) *(20)*. Stem height was 5.6 cm (2.2 in) the first year and 9.4 cm (3.7 in) the second year.

Cold storage of autumn-lifted basswood seedlings maintains root growth capacity and overall seedling vigor for spring planting. Autumn-lifted stock should be stored at a temperature of 5° C (41° F) and a relative humidity of 70-85 percent *(46)*.

Basswood has been successfully planted in Ontario on cutover land and abandoned farmland. On cutover land, survival was best when a light overhead canopy (8.0 m^2/ha or 35 ft^2/acre of residual basal area) controlled competing vegetation *(36)*. Release of the seedlings from the residual overstory and undergrowth was recommended after three growing seasons. Fall plantings failed to survive. Early failures of hardwoods planted on old-field sites in Ontario have been attributed to the absence of mycorrhizal fungi *(30)*, insufficient site preparation, and insufficient postplanting weed control *(42,44)*. Fertilization at the time of planting had little effect on seedling survival or growth *(43)*.

Vegetative Reproduction—Basswood (fig. 3) sprouts prolifically, and this vegetative regeneration can be managed for sawtimber. Sprouts commonly originate on the stump at the ground line, and vigorous sprouts occur over a wide range of diameter classes *(31)*. Almost all trees 10 cm (4 in) in diameter and smaller will produce sprouts and more than half of sawlog-size trees can be expected to produce stump sprouts *(23)*. However, early thinning of stump sprouts (preferably before they reach 5 cm (2 in) d.b.h. or about age 10) is needed to ensure both good quality and rapid growth. Clumps should be thinned to not more than two stems; such thinnings will reduce the incidence of stem degrade due to decay, seams, and sweep *(23,38)*.

Because an extensive root system already exists, a basswood sprout has a higher probability of replacing a parent stem than does a sugar maple seedling. Thus, the ability to produce abundant stump sprouts allows basswood to maintain itself in a stand with the more shade-tolerant maple despite the much larger numbers of sugar maple in the subcanopy *(13)*.

Sapling and Pole Stages to Maturity

Growth and Yield—This species reaches a height of 23 to 40 m (75 to 130 ft) with a d.b.h. of 91 to 122 cm (36 to 48 in). Under favorable conditions, trees sometimes attain a height of 43 m (140 ft) and a d.b.h. of 137 cm (54 in). Estimates of maximum longevity generally exceed 200 years.

Basswood grows faster than most other northern hardwood species. On the same site, basswood often exceeds sugar maple and yellow birch *(Betula alleghaniensis)* in site index by 1.5 m (5 ft) and beech by 3 m (10 ft) *(11)*.

Diameter growth for basswood averaged 3 mm (0.11 in) per year in three unmanaged stands in northeastern Wisconsin (site index at base age 50 years for basswood of 21.3 m or 70 ft). The same site under managed conditions produced substantially higher growth rates. Annual diameter growth average for a crop tree release was 4.6 mm (0.18 in); for a 20.7 m^2 and 17.2 m^2/ha (90 ft^2 and 75 ft^2/acre) (residual sawtimber) selection cut, it was 3.8 and 4.8 mm (0.15, 0.19 in); and for a group selection cut, it was 3 mm (0.12 in). Relatively narrow bark ridges and V-shaped fissures, with new light-colored inner bark visible in the fissures, represent a high-vigor basswood. In contrast, low-vigor trees have scaly bark with wide bark ridges and shallow, short fissures, frequently producing a rather smooth surface *(12)*.

Two phases can be noted in the renewal of cambial activity for basswood. The first phase is the reactivity of cambium that occurs independently of the initial meristematic activity within the overwintering buds. The second phase, accelerating cambial activity after bud-break, is presumably under the influence of primary growth *(14)*. Winter stem contraction for basswood often exceeds stem expansion from the previous growing season. The amount of winter shrinkage in basswood stems was greater than that of yellow birch, sugar maple, or hemlock *(Tsuga canadensis) (49)*.

The period of shoot elongation for basswood in northern areas is shorter than that for other hardwoods—only red oak and sugar maple had shorter periods of terminal shoot elongation among seven species studied in northern Wisconsin. Based on an average of three growing seasons, shoot elongation for basswood began in May and was completed by the first of June *(10)*. Longer periods of shoot elongation have been noted for open-grown basswood in Illinois and basswood plantations in Ontario (mid-May to mid-August). Chlorophyll is found in xylem rays and primary xylem of basswood twigs *(47)*. Although the photosynthetic contribution is not large, it may have seasonal significance when leaves are absent.

Rooting Habit—The initial taproot observed in basswood seedlings gives way in saplings to a system of lateral roots *(5)*. This early root development is gradually obscured by the intensive development of

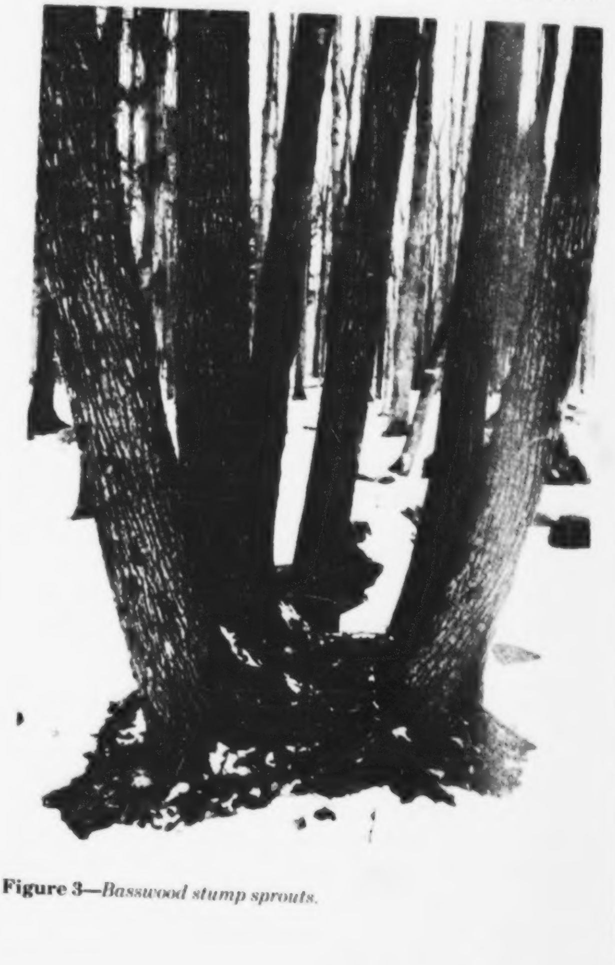

Figure 3—*Basswood stump sprouts.*

oblique roots in the central mass, and surface lateral roots extend out from this mass *(16)*. Adventitious roots have developed on the lower stem of basswood engulfed by dune sand *(4)*.

Reaction to Competition—Although basswood is less shade tolerant than its common associate, sugar maple, vigorous sprouting and rapid sprout growth allow it to persist under the selection system. Overall, American basswood is most accurately classed as tolerant of shade. This great sprouting vigor also helps it compete with the abundant regrowth following clearcutting. On an excellent site in the central Appalachian hardwoods, basswood was second only to sugar maple in number of stems 7 years after clearcutting. On a good site and a fair site, however, basswood was not among the five most numerous species during the same period *(39)*.

For reproduction from seed, the shelterwood system should provide the partial shade necessary to control competing vegetation, and to create a microclimate suitable for germination. After basswood is established, the overstory should be removed.

Closely spaced, forest-grown trees develop straight, columnar trunks and narrow crowns, but open-grown trees have short stems and many large branches.

Damaging Agents—Basswood plantations established on weed-infested old-field sites are susceptible to girdling by mice and voles, and completely girdled trees die. In a southern Ontario plantation, 44 percent of the basswood stems were completely girdled and 39 percent were partially girdled *(41)*. The species responsible for the girdling, the meadow vole, does most of this damage feeding beneath the snow. Rabbits also feed heavily on seedlings and small saplings in both plantations and natural stands. Basswood seeds are eaten by mice, squirrels, and chipmunks, thus reducing the chances of seedling establishment.

Many different insects attack basswood, but few serious insect problems exist. The linden borer *(Saperda vestita)* makes long, irregular tunnels, particularly at the base of the tree, and may damage weak, very young, or overmature trees. Local infestations of defoliators may occur. The primary ones include the linden looper *(Erannis tiliaria)*, basswood leafminer *(Baliosus nervosus)*, spring cankerworm *(Paleacrita vernata)*, fall cankerworm *(Alsophila pometaria)*, whitemarked tussock moth *(Orgyia leucostigma)*, gypsy moth *(Lymantria dispar)*, and forest tent caterpillar *(Malacosoma disstria)* *(1,22)*. In New England, American basswood is a highly preferred host for gypsy moth *(21)*, while in southern Quebec, it was classified as intermediate in susceptibility to gypsy moth defoliation *(27)*.

The foliage is host to various diseases—anthracnose *(Gnomonia tiliae)*, black mold *(Fumago vagans)*, and leaf spot *(Cercospora microsora)*—but none seem to do serious damage. The wood of basswood decays easily and once exposed can be host to many of the common hardwood decay organisms such as the yellow cap fungi *(Pholiota limonella)* and *Collybia velutipes*. *Phellinus igniarius*, *Ustulina deusta*, and nectria canker *(Nectria galligena)* also are found on basswood.

Little defect is encountered in basswood when harvested before it reaches 120 years of age. Beyond this age, the chances of losses due to decay are greatly increased. Cull studies in the forests of Ontario indicate that yellow-brown stringy rot was the most common bole defect encountered; brown stain, some incipient yellow rot, and green stain were also found *(8)*.

The thin bark of this species is easily damaged by fire *(13)*. Basswood is one of the hardwoods least susceptible to late spring frosts *(40)*.

Special Uses

Basswood has relatively soft wood that works exceptionally well and is valued for hand carving. The inner bark, or bast, can be used as a source of fiber for making rope or for weaving such items as baskets and mats. Basswood flowers produce an abundance of nectar from which choice honey is made. In fact, in some parts of its range basswood is known as the bee-tree. Throughout the Eastern United States, basswood is frequently planted along city streets.

Genetics

The number of native taxa in the genus *Tilia* has been debated for some time. As many as 15 native species and 13 varieties are named in early taxonomic work. Only three species of *Tilia* are now recognized in the United States, *T. americana* L., *T. caroliniana* Mill., and *T. heterophylla* Vent. *(24)*. Recent studies, however, suggest that the genus *Tilia* in eastern North America should be considered a single, but highly variable, species. In sampling *Tilia* from Quebec, Canada, to Lake County, FL, no apparent morphological discontinuities between populations were found to justify delimitation at the species level *(20)*.

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Tilia heterophylla Vent. White Basswood

Tiliaceae Basswood family

Timothy LaFarge

White basswood (*Tilia heterophylla*) is a medium-sized tree of the upper Piedmont region and the Appalachian Mountains where it grows on moist, well-drained soils in coves or along mountain streams with other hardwoods. Its growth is moderately fast and it produces commercially valuable lumber. The soft, lightweight wood is used for cabinetry, woodenware, and pulpwood, among its many uses. The name beetree linden is common because of the extensive use of this tree by bees for honey production. It is also an attractive landscape tree.

Habitat

Native Range

The range of white basswood (fig. 1) extends from southwestern Pennsylvania west in southern Ohio,

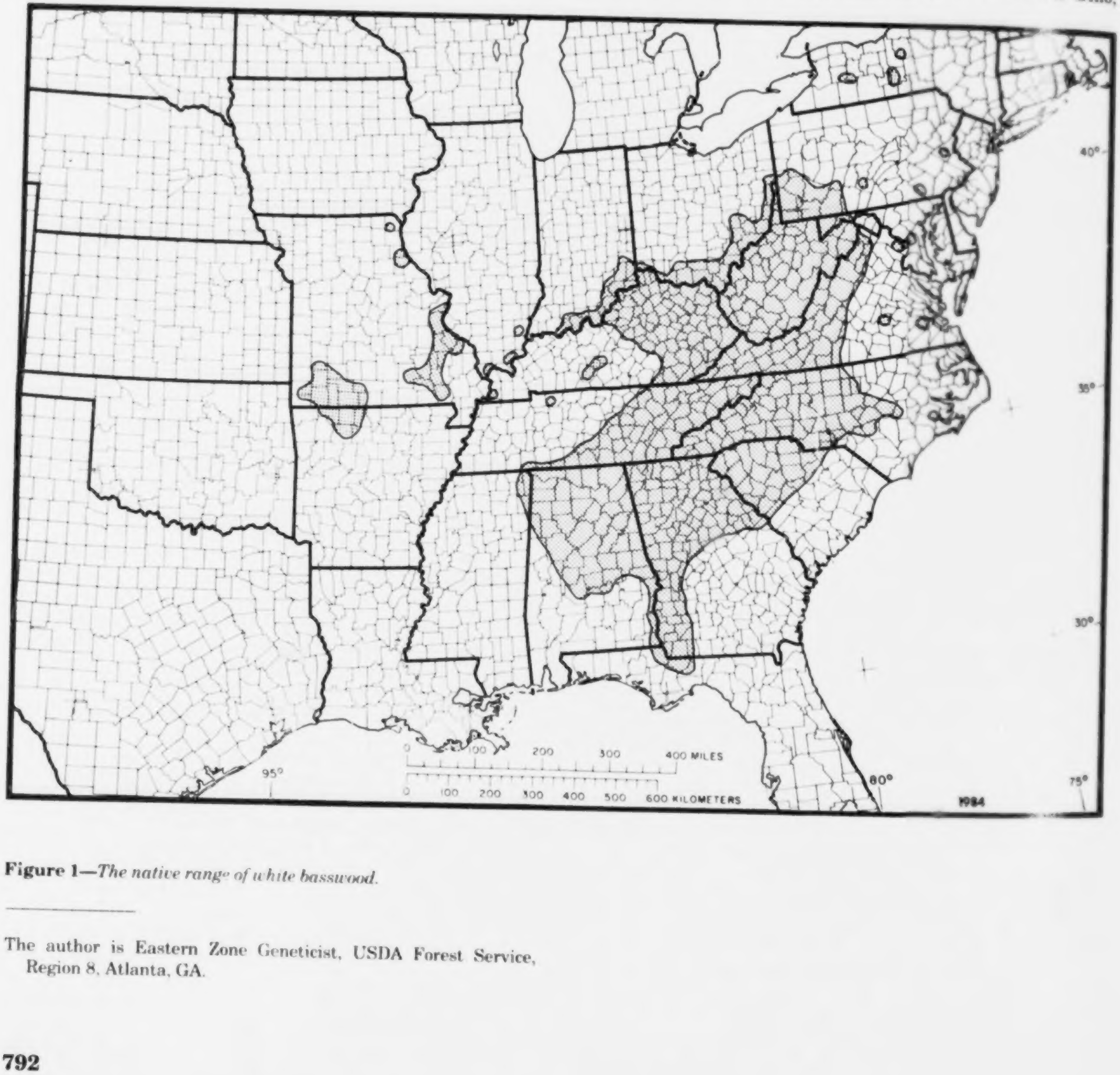

Figure 1—*The native range of white basswood.*

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Indiana, and Illinois to Missouri; south to northern Arkansas; east to northeastern Mississippi, Alabama, northwestern Florida, and Georgia; and north to Maryland. Outlying populations occur in eastern Pennsylvania and western New York. It reaches its largest growth in the Appalachian Mountains, where it is often dominant. However, it is most common in the mixed mesophytic forests of the Cumberland Plateau, where it is second only to sugar maple (*Acer saccharum*) in frequency (*10,11*).

Climate

Climatic conditions vary widely within the range of white basswood. In its southernmost range in northwest Florida, the mean annual number of days below freezing is 20; at the northernmost extremes in Pennsylvania and western New York, it is 150. These extremes occasionally include temperatures below -18° C (0° F) in the winter and some days in excess of 38° C (100° F) in the summer. Annual precipitation varies widely, ranging from more than 2030 mm (80 in) in some areas in the Southern Appalachians to about 910 mm (36 in) in some northern and western margins of its range (*14*).

Soils and Topography

Quite particular in its soil and moisture requirements, white basswood cannot tolerate very wet or very dry conditions, and it almost always grows on moist but well-drained soils. This tree grows best along mountain streams or in mountain coves where the soils have an alluvial or a colluvial origin. These soils are deep, friable, and have considerable humus (*11*).

White basswood is found on soils of five orders, Inceptisols, Ultisols, Alfisols, Entisols, and Mollisols. Of these, Inceptisols and Ultisols occupy by far the largest areas, and their common property is moisture availability for more than half the year or for more than 3 consecutive months during the warm season. Moisture availability during the warm season is also a property of Alfisols, which are present in the western portions of the range of white basswood, but it is not a property of Entisols and Mollisols. However, the latter orders occupy very small areas in the southern and western margins of the species range (*13*).

Although rare at very low elevations, basswood is occasionally found on the Coastal Plain but appears with increasing frequency in the upper Piedmont. It is common in the Appalachian Mountains at elevations between 900 m (3,000 ft) and 1500 m (5,000 ft), where it usually grows on north and east exposures and on flood plains or in deep, moist coves (*11*).

Associated Forest Cover

White basswood is a component of five forest cover types (*5*): White Oak–Black Oak–Northern Red Oak (Society of American Foresters Type 52), Yellow-Poplar (Type 57), Yellow-Poplar–Eastern Hemlock (Type 58), Yellow-Poplar–White Oak–Northern Red Oak (Type 59), and Silver Maple–American Elm (Type 62). However, it is not a major species in any of them. In the northern part of its range it grows with northern red oak (*Quercus rubra*), white ash (*Fraxinus americana*), black cherry (*Prunus serotina*), white oak (*Q. alba*), black oak (*Q. velutina*), sweet birch (*Betula lenta*), butternut (*Juglans cinerea*), American elm (*Ulmus americana*), American Beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), eastern hemlock (*Tsuga canadensis*), and hickories (*Carya* spp.); farther south in the Appalachians it is more commonly found with yellow buckeye (*Aesculus octandra*), yellow birch (*B. alleghaniensis*), sweet birch, sugar maple, black cherry, yellow-polar (*Liriodendron tulipifera*), cucumbertree (*Magnolia acuminata*), black locust (*Robinia pseudoacacia*), loblolly pine (*Pinus taeda*), and shortleaf pine (*P. echinata*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—White basswood flowers in the latter part of June and early July. Once flowering begins, flowers, pollen, and nectar are abundant. The perfect flowers are protandrous; the anthers usually open in the afternoon and release pollen for 24 hours, after which the stigmas become receptive and nectar production begins. There are 66 insect species known to pollinate basswood; bees and flies are the most common diurnal visitors and moths the principal nocturnal visitors. Nocturnal pollinators produce somewhat less fruit set than diurnal pollinators. Although insect pollination is predominant, wind pollination plays a minor role. White basswood is not self-compatible (*1*).

The fruits are nutlike, leathery or woody, ellipsoidal, about 13 mm (0.5 in) long, and covered with rust-brown, woolly hairs. The fruits are borne in clusters of six or seven on bracts. The bracts, which are shaped like long, slender leaves, may serve as wings for the purpose of wind dispersal or may function primarily as flags to attract nocturnal pollinators. The light-colored bracts are distinct against the dark foliage at night *(1)*.

Seed Production and Dissemination—White basswood seeds ripen in September and October following pollination and are dispersed in the winter and spring. Little information exists on fruit set and seed dispersal of this species. In general, these events seem to differ little from those of American basswood (*Tilia americana*) *(11)*.

As with most tree seeds, natural germination is best on mineral soil. No specific information is available for white basswood, but in general, basswood seeds may remain dormant for as long as 2 or 3 years *(12)*.

Seedling Development—Little is known about the early growth of white basswood. Immediate sowing after early collection of American basswood fruits (when they first turn slightly brown) has been found to give good germination success. Germination is epigeal. Basswood seedlings are usually planted as 1-0 or 2-0 stock *(12)*.

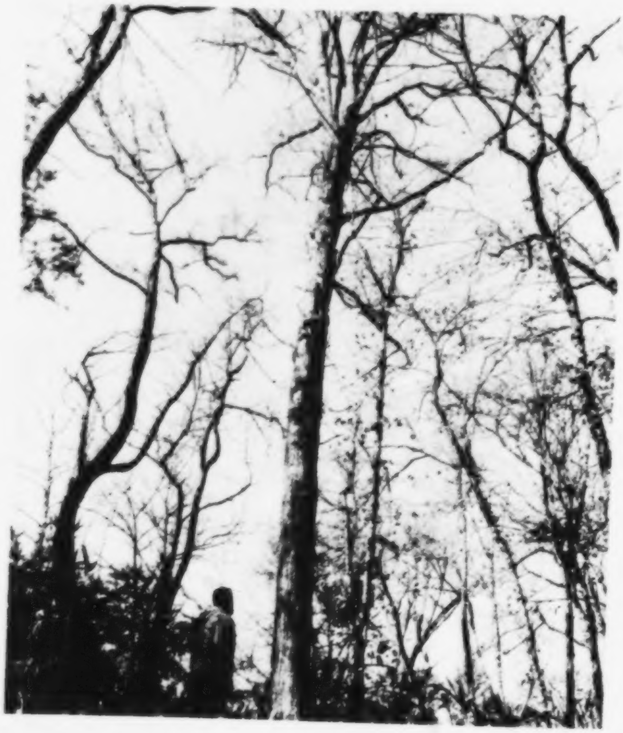

Figure 2—*A white basswood on Hitchiti Experimental Forest, Jones County, GA.*

Vegetative Reproduction—White basswood sprouts vigorously and commonly grows in clumps of three to six or more stems. Although clump growth is good, the trees are frequently defective and susceptible to sleet and wind damage. Hence, stands of sprouts are less desirable than those of seedling origin *(11)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature white basswood may exceed 27 m (90 ft) in height and 91 cm (36 in) in d.b.h. Typically, the bole is free of branches, smooth, and cylindrical (fig. 2). The growth rate of basswood is intermediate compared with other southern Appalachian species; it grows faster than most of the oaks and maples, but considerably slower than yellow-poplar and northern red oak. Economic maturity for sawtimber is estimated to be a d.b.h. of between 43 and 61 cm (17 and 24 in), depending on the vigor class of the tree *(11)*.

No volume or yield tables are available for white basswood. A standing inventory of basswood—including net annual growth, removals, and mortality—is available for five Southeastern States (table 1). Although white basswood is not distinguished from American basswood in this survey, the latter species grows only in the northern and westernmost portions of Virginia and North Carolina. White basswood grows in all five States.

Table 1—Volume of standing basswood in the Southeast[1,2]

Location	Standing volume	Annual		
		Net growth	Removals	Mortality
			thousand m³	
Florida	664.4	18.4	11.2	10.6
Georgia	416.8	9.8	2.9	—
S. Carolina	44.9	4.0	—	3.8
N. Carolina	2227.2	63.8	5.6	6.0
Virginia	3760.5	108.3	16.7	23.2
Total	7113.8	204.3	36.4	43.6
			thousand ft³	
Florida	23,478	650	397	374
Georgia	14,729	348	103	—
S. Carolina	1,588	140	—	134
N. Carolina	78,699	2,253	198	213
Virginia	132,881	3,827	589	820
Total	251,375	7,218	1,287	1,541

[1] Volume of stemwood from a 0.3 m (1 ft) stump to a 10 cm (4 in) diameter top, outside bark.
[2] Personal communication, Herbert A. Knight, resource analyst, Southeastern Forest Experiment Station, Asheville, NC.

Rooting Habit—White basswood roots have been found to have ectotrophic mycorrhizae; a fungus grows on the outside of the short root to form a mantle, and two rows of spherical cells are present in the cortex to form a Hartig net *(8)*.

Reaction to Competition—Basswood is classed as shade tolerant, and variations between American basswood and white basswood are not noted *(11)*.

Damaging Agents—White basswood is relatively free of serious diseases, although it is attacked by cankers, rots, stains, leaf spots, and wilt. Discolorations of the wood are common following wounding of any type, but they are not considered serious defects unless decay enters before the wound heals. Decay fungi attacking white basswood include species of *Daedalea, Fomes, Hydnum, Pholiota, Pleurotus, Polyporus, Irpex,* and *Stereum*. Basswoods of stem sprout origin or seedlings that have been wounded are likely to become highly defective; often the main bole of such trees will be almost entirely hollow *(6,11)*.

Cankers caused by *Nectria galligena* are common on basswood but are not considered serious problems. Other stem diseases of minor importance are *Nectria cinnabarina, Botryosphaeria ribis,* and *Strumella coryneoidea*.

Leaf spots are common but do not cause excessive damage. The common leaf spots are caused by species of *Cercospora, Phyllosticta, Gnomonia, Phlyctaena,* and *Asteroma*. Wilt caused by species of *Verticillium* is known to occur in white basswood but so far has been of no consequence in forest stands *(6,11)*.

White basswood is also comparatively free of serious insect enemies, but it is the host of many defoliators, several borers, aphids, and gall midges. Common defoliators include the basswood leafroller *(Pantographa limata)*, elm spanworm *(Ennomos subsignaria)*, linden looper *(Erannis tiliaria)*, white-marked tussock moth *(Orgyia leucostigma)*, variable oakleaf caterpillar *(Heterocampa manteo)*, basswood leafminer *(Baliosus nervosus)*, bagworm *(Thyridopteryx ephemeraeformis)*, and the Japanese beetle *(Popillia japonica)*.

Important borers include the linden borer *(Saperda vestita)*, *Chrysobothris azurea*, flatheaded sycamore-heartwood borer *(Chalcophorella campestris)*, which enters the wood at wounds, *Dicerca lurida*, ambrosia beetles *(Platypus compositus)*, and the twig girdler *(Oncideres cingulata) (3)*.

Like those of yellow-poplar, the tender twigs and smaller branches of basswood are readily browsed by livestock and white-tailed deer.

Because of its thin bark, basswood is very susceptible to fire damage, especially at the seedling and sapling size. Consequently, butt rot is very common and a serious problem in burned stands.

Special Uses

Because of its soft texture, light weight, and dimensional stability, basswood lumber (including that of white basswood) is a choice wood. In addition to lumber uses, it is highly desirable for veneer, slack cooperage, excelsior, drawing boards, and particleboard; other values include bee pasture, yielding a fragrant honey, and shade and ornamental plantings *(12)*.

Genetics

Currently three species of *Tilia* in North America are recognized: *T. americana, T. heterophylla*, and *T. caroliniana (9,10)*, although there are no known races or varieties within them. Recent studies of field specimens, field plots, and nursery plantings indicate that the variation in *Tilia* is essentially clinal. Pubescence and stellate hairs tend to be absent in the northwest portions of the ranges of basswoods but abundant in South Carolina *(2)*. Flavonoid variation patterns indicate definite differences between northern and southern populations and show an intermediate zone in the southern Appalachians *(7)*. These patterns suggest that there is only one species, *Tilia americana* L., in the range from Massachusetts to North Carolina. The population occupying the remaining southeastern portion of the range could be named *T. americana* var. *heterophylla*.

Hybrid swarms between white basswood and other species have been observed outside the glaciated area in southern Ohio *(4)*. It has also been suggested that the absence of distinct morphological differences between species of basswood leads to inconstancy of insect pollinators and hence to hybridization *(1)*.

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Ulmus alata Michx. Winged Elm

Ulmaceae Elm family

G. A. Snow

Winged elm *(Ulmus alata)* is a very hardy, small- to medium-sized tree in a wide range of habitats throughout much of the southern Midwest and Southeastern United States. Other common names are cork elm and wahoo.

On fertile soils with adequate moisture and drainage, winged elm grows well and is a useful component of several forest types. On poor dry sites it is stunted and gnarled and can be an undesirable invader of grazing land. Winged elm lumber is mixed with other elm. This tree is occasionally planted in southern landscapes.

Habitat

Native Range

Winged elm (figs. 1, 2) extends from southern Virginia west to Kentucky, southern Indiana and Illinois, and central Missouri; south to central Ok-

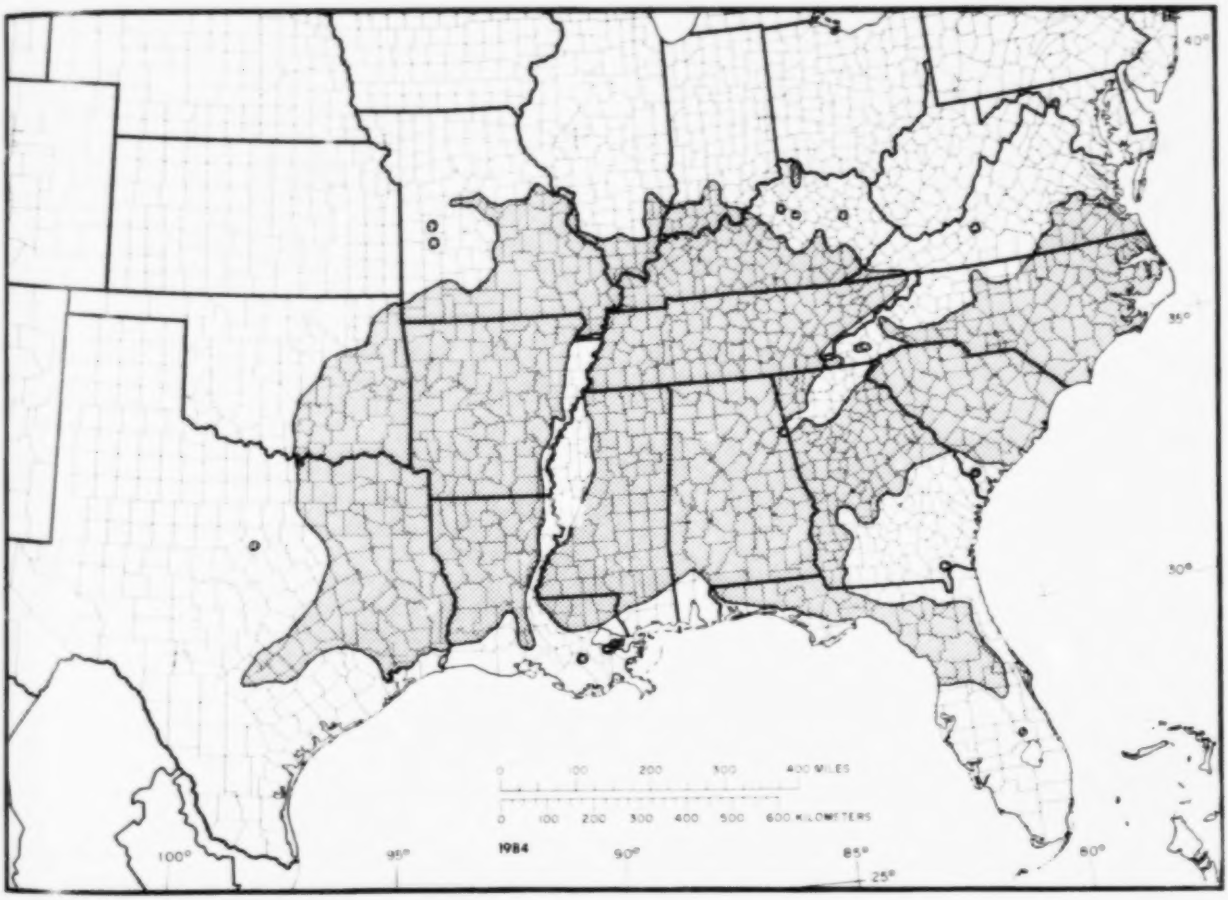

Figure 1—*The native range of winged elm.*

The author is Principal Plant Pathologist, Southern Forest Experiment Station, New Orleans, LA.

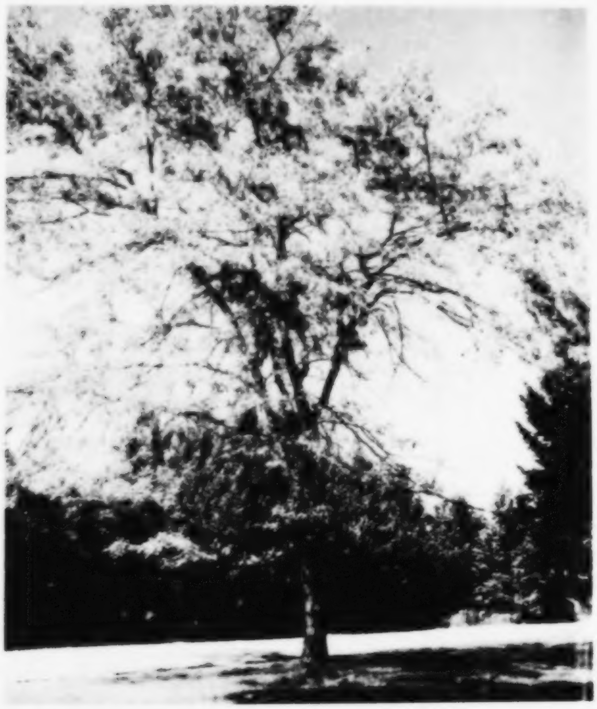

Figure 2—*Winged elm.*

lahoma and southeastern Texas; and east to central Florida. It is also found locally in Maryland *(10,14)*.

Climate

Within the natural range of winged elm, the climate varies from warm in the South to moderately cold in the North *(20)*. The region is principally within the humid climatic province of the southeastern United States. Annual precipitation averages 1020 to 1520 mm (40 to 60 in); half or more of this occurs during the growing season, April to September. Throughout the greater portion of the tree's range, the growing season averages from 180 to 300 days, and average annual temperatures are from 13° to 21° C (55° to 70° F). Average annual snowfall is from 38 cm (15 in) in the North to none in the South.

Soils and Topography

Winged elm is found on a great variety of soils. It grows fairly well on dry as well as on rich, moist soils. The species does particularly well in the silty uplands in Mississippi where site index values at base age 50 years are 21.3 to 27.4 m (70 to 90 ft) on Memphis soils *(4)*. On the Delta bottom lands it grows on terrace flats with tight silty soils of the order Inceptisols. In southern Illinois, it grows in old abandoned fields and along fence rows on upland clay soils. The species is generally associated with intermittent streams and other moist, lower slope sites. In the hill country of Tennessee and North Carolina, it may be found on upper or middle slopes, however. It is listed in forest types that are found at elevations up to 760 m (2,500 ft). The species is also common on sandy soils in bottom lands near Dallas, TX *(11)*. Overall, winged elm is most commonly found on soils of the orders Alfisols and Ultisols.

Associated Forest Cover

Winged elm generally grows only as scattered trees in mixture with other hardwoods *(14)*. It is not a major component of any forest cover type in the Eastern United States, but it is found in varying amounts in four major types *(17)*: Post Oak–Blackjack Oak (Society of American Foresters Type 40), White Oak–Black Oak–Northern Red Oak (Type 52), Swamp Chestnut Oak–Cherrybark Oak (Type 91), and Sugarberry–American Elm–Green Ash (Type 93).

In the southern part of the Central Forest Region, winged elm occurs as a minor species in Post Oak–Blackjack Oak. From the Central Forest Region southward through Tennessee, Arkansas, Mississippi, and Alabama it is associated with White Oak–Black Oak–Northern Red Oak. In the Southern Forest Region and within flood plains of major rivers, winged elm is found in either Swamp Chestnut Oak–Cherrybark Oak or in Sugarberry–American Elm–Green Ash. Here, associated understory trees are eastern hophornbeam *(Ostrya virginiana)*, American hornbeam *(Carpinus caroliniana)*, and American holly *(Ilex opaca)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The perfect flowers of winged elm are borne on threadlike pedicels in short, few-flowered drooping fascicles before the leaves appear in March and April *(22)*. The fruit is a reddish or greenish samara, ovate to oblong and 6 to 8 mm (0.25 to 0.33 in) long. Fruits ripen in April and seeds are dispersed the same month *(3)*. The seed is solitary and it and its wing are flat and hairy, especially on the margin. The reddish samaras give the tree a reddish appearance when fruiting.

Seed Dissemination—Seeds are disseminated by wind and water. They are eaten by a variety of birds and small animals which likely serve as another means of dissemination.

Seedling Development—Germination is epigeal *(3)*. The cotyledons are oval with shallowly notched apexes and heart-shaped bases *(9)*. They are light green and smooth on both surfaces and persist on the plant for 1 to 2 months. The first leaves appear within 1 week after germination. They are small and sharp-pointed and have typical elm venation. The stem is circular, zig-zag, and slightly hairy to smooth. Two corky wings develop opposite each other on the stem late in the first year. The buds are slender and sharp-pointed, chestnut brown, slightly hairy, and 1.6 mm (0.06 in) long.

Winged elm is a light-demanding species and reproduction is often sparse in an understory *(1)*. It is an invader of forest openings, old fields, and rangelands. It survives grazing as bushes and sprouts prolifically *(15)*. Winged elm is difficult to kill with herbicides and its eradication has been the subject of several rangeland studies during the past decade *(18)*.

Vegetative Reproduction—No information is currently available on the sprouting and rooting habits of winged elm.

Sapling and Pole Stages to Maturity

Growth and Yield—Winged elm is a medium-sized tree, usually 12 to 15 m (40 to 50 ft) in height but occasionally 24 to 30 m (80 to 100 ft), and is rarely more than 61 cm (24 in) in d.b.h. This species develops a short bole with branches ascending into a fairly open, round-topped crown. It has a lacy, or somewhat drooping habit. One special characteristic is the corky, persistent wings or projections often found on the branches. Winged elm grows rapidly in the open. Under forest conditions its growth rate is usually considered poor in relation to its associates. Diameter growth in a natural stand averages 50 to 64 mm (2.0 to 2.5 in) in 10 years *(12)*.

Rooting Habit—No information available.

Reaction to Competition—Of all species of elms native to the United States, winged elm is perhaps the least tolerant of shade. It is, nevertheless, classed as a shade tolerant species *(15)*. Normally, winged elm is not associated with standing water except in intermittent pools and shallow sheets of water after heavy rains. Winged elm is classified as tolerant of flooding *(19)*.

Damaging Agents—A large variety of insects and diseases are reported for winged elm *(2,7,8)*. This is not because the species is generally more susceptible to pathogens than other native hardwoods. The primary reason is that the species is susceptible to *Ceratocystis ulmi*, which causes Dutch elm disease, and to the mycoplasmalike organism which causes elm phloem necrosis. Both have been devastating to the elms native to North America and since these diseases are both transmitted by insects, a large amount of research has been done on all insects and diseases of elms in the United States. The Dutch elm disease is most prevalent across the northern portion of the natural range of winged elm. As of 1976, it had not been found in Louisiana and Florida *(21)*. Phloem necrosis was distributed throughout much of the north and central range of winged elm by 1975 *(6)*. Both diseases have spread into the Southeastern States from the north; whether or not the warmer climate or other factors in these States will eventually stop the epidemics remains uncertain.

Special Uses

For commercial purposes the wood of winged elm is classed as hard elm or rock elm *(5,13)*. Elm wood is used principally for furniture, hardwood dimension and flooring, boxes, and crates. Elm's excellent resistance to splitting has made it a choice wood for the manufacture of high quality hockey sticks. The manufacture of furniture continues to increase the demand for elm for bent parts of chairs such as rockers and arms.

The mast from winged elm is eaten by birds and animals, and the twigs and leaves are important for white-tailed deer *(16)*. Both twigs and leaves are most succulent, nutritious, and digestible during spring and are less useful as food the rest of the year because after abscission, the leaves lose most of their quality and digestibility.

Genetics

Winged elm has little commercial value. As a consequence, no attempts to hybridize or improve the species have been reported.

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Ulmus americana L. American Elm

Ulmaceae Elm family

Calvin F. Bey

American elm *(Ulmus americana)*, also known as white elm, water elm, soft elm, or Florida elm, is most notable for its susceptibility to the wilt fungus, *Ceratocystis ulmi*. Commonly called Dutch elm disease, this wilt has had a tragic impact on American elms. Scores of dead elms in the forests, shelterbelts, and urban areas are testimony to the seriousness of the disease. Because of it, American elms now comprise a smaller percentage of the large diameter trees in mixed forest stands than formerly. Nevertheless, the previously developed silvical concepts remain basically sound.

Habitat

Native Range

American elm (figs. 1, 2) is found throughout Eastern North America. Its range is from Cape Breton Island, Nova Scotia, west to central Ontario, southern Manitoba, and southeastern Saskatchewan; south to extreme eastern Montana, northeastern Wyoming, western Nebraska, Kansas, and Oklahoma into central Texas; east to central Florida; and north along the entire east coast.

Climate

Within the natural range of American elm, the climate varies from warm and humid in the southeast to cold and dry in the northwest. Average temperatures are as follows: January, from -18° C (0° F) and below in Canada and 16° C (60° F) in central Florida; July, from 16° C (60° F) in Manitoba to 27° C (80° F) in the Southern States; annual maximum, 32° C (90° F) to 35° C (95° F) in the Northeast and 38° C (100° F) to 41° C (105° F) in the South and West; annual minimum, from -40° C (-40° F) to -18° C (0° F) in the North and -18° C (0° F) to -1° C (30° F) in the South.

Average annual precipitation varies from a scarce 380 mm (15 in) in the Northwest to a plentiful 1520 mm (60 in) on the gulf coast. Over the central part of the species range there are about 760 to 1270 mm (30 to 50 in) per year. Throughout the range most of the precipitation comes during the warm (April–September) season. Average annual snowfall generally varies from none in Florida to about 200 cm (80 in) in the Northeast. A few areas, mainly around the Great Lakes, get 254 to 380 cm (100 to 150 in) of snow per year.

The average frost-free period is about 80 to 160 days for the northern tier of States and Canada to about 200 to 320 days for the gulf coast and Southeastern States.

Soils and Topography

American elm is most common on flats and bottom lands throughout its range but is not restricted to these sites. On the southern bottom-land region, it is found widely in first bottoms and terraces, especially on first bottom flats, but not in deep swamps. At higher elevations in the Appalachians, it is often limited to the vicinity of large streams and rarely appears at elevations above 610 m (2,000 ft). In West Virginia, however, it does appear in high coves at elevations of 760 m (2,500 ft). In the Lake and Central States, it is found on plains and morainal hills as well as on bottom lands and swamp margins. Along the northwestern edge of the range, it is usually restricted to valley bottoms along watercourses.

Although American elm is common on bottom-land soils, it is found on many of the great soil groups within its range. The soils include well-drained sands, organic bogs, undifferentiated silts, poorly drained clays, prairie loams, and many intermediate combinations.

American elm grows best on rich, well-drained loams. Soil moisture greatly influences its growth. Growth is poor in droughty sands and in soils where the summer water table is high. In Michigan, on loam and clay soils, growth is good when the summer water table drops 2.4 to 3.0 m (8 to 10 ft) below the surface, medium with summer water table at 1.2 to 2.4 m (4 to 8 ft), and poor when topsoil is wet throughout the year. On sandy soils underlain with clay, growth is medium to good where the summer water table is 0.6 m (2 ft) or more below the soil surface. Organic soils are usually poor sites, but those with a summer water table at least 0.6 m (2 ft) below the surface are classed as medium sites for American elm.

In the South, American elm is common on clay and silty-clay loams on first bottoms and terraces; growth is medium on wetter sites and good on well-drained flats in first bottoms *(8)*. In the arid western end of the range, it is usually confined to the silt or clay

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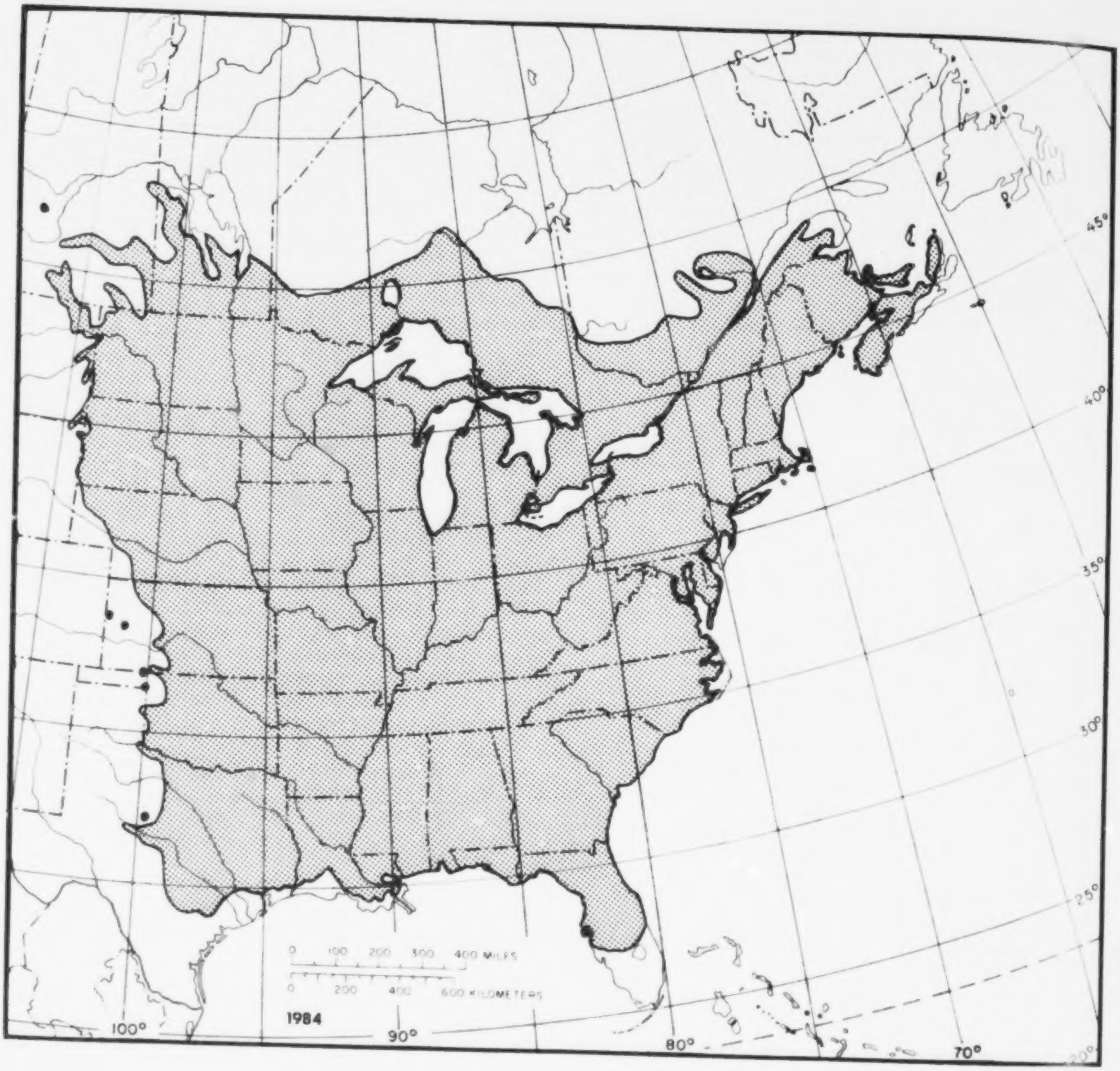

Figure 1—*The native range of American elm.*

loams in river bottoms and terraces. In shelterbelt plantings on the uplands, however, survival is generally best on sandy soils where the moisture is more evenly distributed to greater depths than in fine-textured soils. American elm most commonly grows on soils of the orders Alfisols, Inceptisols, Mollisols, and Ultisols.

Soil acidity under stands of American elm varies from acid on some of the swamp margin sites in the Lake States to mildly alkaline on the prairie soils. A soil reaction considered suitable for this species ranges from pH 5.5 to 8.0.

Leaf litter of American elm decomposes more rapidly than that of sugar maple (*Acer saccharum*),

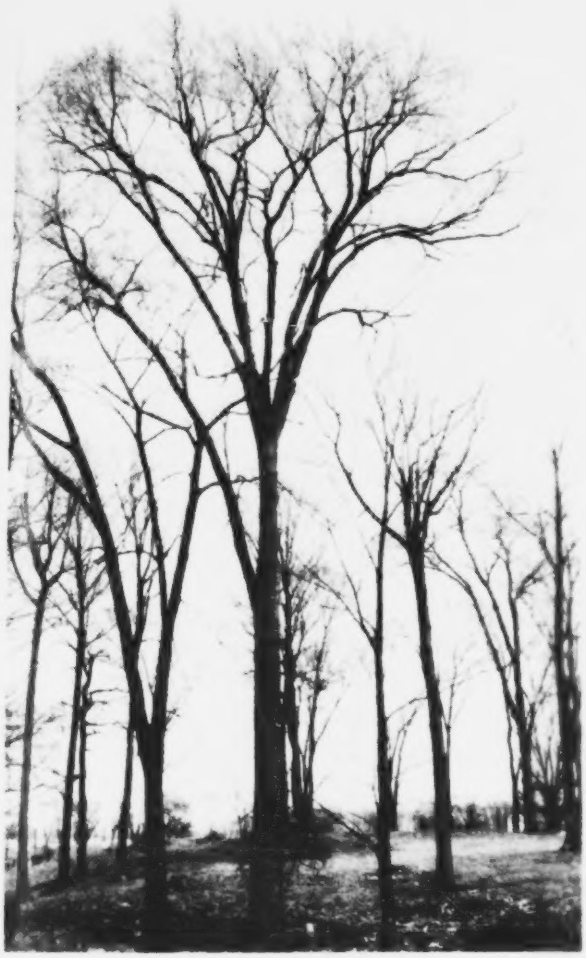

Figure 2—*Forest-grown American elm.*

shagbark hickory *(Carya ovata)*, white oak *(Quercus alba)*, and northern red oak *(Q. rubra)*. Under Missouri conditions, the leaves crumble readily after 18 months on the ground. They have a relatively high content of potassium and also of calcium (1 to 2 percent). Because its litter decomposes rapidly and contains many desirable nutrients, American elm is considered a "soil-improving" species.

Associated Forest Cover

Throughout its range, American elm seldom grows in pure stands and is usually found in mixture with other species. It is a major component of four forest cover types: Black Ash–American Elm–Red Maple (Society of American Foresters Type 39), Silver Maple–American Elm (Type 62), Sugarberry–American Elm–Green Ash (Type 93), and Sycamore–Sweetgum–American Elm (Type 94). It is a minor component in 20 other forest types.

Black Ash–American Elm–Red Maple (Type 39) appears throughout the Northern Forest and into the Boreal Forest in Canada, and throughout the Lake States and into the northern edge of the Central Forest. In this type the most common associates, other than the type species, are as follows: In the Lake States and Canada, balsam poplar *(Populus balsamifera)*, balsam fir *(Abies balsamea)*, and yellow birch *(Betula alleghaniensis)*; in Ohio and Indiana, silver maple *(Acer saccharinum)*, swamp white oak *(Quercus bicolor)*, sycamore *(Platanus occidentalis)*, pin oak *(Quercus palustris)*, black tupelo *(Nyssa sylvatica)*, and eastern cottonwood *(Populus deltoides)*; in New England and eastern Canada, sweet birch *(Betula lenta)*, paper birch *(B. papyrifera)*, gray birch *(B. populifolia)*, silver maple, and black spruce *(Picea mariana)*; and in New York, white ash *(Fraxinus americana)*, slippery and rock elms *(Ulmus rubra* and *U. thomasii)*, yellow birch, black tupelo, sycamore, eastern hemlock *(Tsuga canadensis)*, bur oak *(Quercus macrocarpa)*, swamp white oak, and silver maple.

Silver Maple–American Elm (Type 62) is common throughout the Central Forest and extends into Canada. Major associates in this type are sweetgum *(Liquidambar styraciflua)*, pin oak, swamp white oak, eastern cottonwood, sycamore, green ash *(Fraxinus pennsylvanica)*, and other moist site hardwoods.

Sugarberry–American Elm–Green Ash (Type 93) is found throughout the Southern Forest within the flood plains of the major rivers. Hackberry *(Celtis occidentalis)* replaces sugarberry *(C. laevigata)* in the northern part of the range. Major associates are water hickory *(Carya aquatica)*, Nuttall *(Quercus nuttallii)*, willow *(Q. phellos)*, water *(Q. nigra)*, and overcup *(Q. lyrata)* oak, sweetgum, and boxelder *(Acer negundo)*.

Sycamore–Sweetgum–American Elm (Type 94) appears as scattered stands throughout the Southern Forest region and lower Ohio River Valley. Common associates include green ash, sugarberry, hackberry, boxelder, silver maple, cottonwood, black willow *(Salix nigra)*, water oak, and pecan *(Carya illinoensis)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—The process of flowering, seed ripening and seed fall in American elm takes place in the spring throughout the range. The glabrous flower buds swell early in February in the South and as late as May in Canada. The flowers appear 2 to 3 weeks before leaf flush. Soon after wind pollination occurs, the fruit ripens, and seed fall is usually complete by mid-March in the South and mid-June in the North.

American elm flowers are typically perfect and occur on long, slender, drooping pedicels, about 2.5 cm (1 in) long, in 3- or 4-flowered short-stalked fascicles. The anthers are bright red, the ovary and styles are light green, and the calyx is green tinged with red above the middle. With controlled pollinations, floral receptivity is greatest when stigma lobes are reflexed above the anthers. The trees are essentially self-sterile. A test in Canada showed only 1.5 percent viable seed from self-pollinated flowers. Pollination may be hampered in a wet spring since the flower anthers will not open in a saturated atmosphere *(9)*.

Seed Production and Dissemination—Seed production in American elm may begin as early as age 15 but is seldom abundant before age 40. When mature, American elm is a prolific seed producer. Trees as old as 300 years have been reported to bear seeds. In closed stands, seed production is greatest in the exposed tops of dominant trees. The winged seeds are light and readily disseminated by the wind. Although most seeds fall within 91 m (300 ft) of the parent tree, some may be carried 0.4 km (0.25 mi) or more. In river-bottom stands, the seeds may be waterborne for miles. Cleaned but not dewinged seeds average 156,000/kg (70,900/lb).

Adverse weather may reduce the seed crop. Spring frosts can injure and kill both flowers and fruit. Observations in Minnesota showed that while nearly ripe seeds were not injured by night temperatures of -3° C (27° F) for several successive nights, most were killed a week later when the temperature dropped to -7° C (19° F) and remained below freezing for 60 hours.

Mammals and birds also may reduce the seed crop. The flower buds, flowers, and fruit are eaten by gray squirrels. The seeds are also eaten by mice, squirrels, opossum, ruffed grouse, Northern bobwhite, and Hungarian partridge.

Seedling Development—Germination in American elm seed is epigeal. It usually germinates soon after it falls, although some seeds may remain dormant until the following spring. While germination may extend over a period of 60 days, most of the seeds germinate in 6 to 12 days. Germination is best with night temperatures at 20° C (68° F) and day temperatures of 30° C (86° F). However, germination is almost as good when daily temperatures range between 10° C (50° F) and 21° C (70° F). Seeds can germinate in darkness, but germination increases in light. Seeds also can lie on flooded ground for as long as 1 month with little adverse effect on germination, except possibly where siltation occurs in flooded bottoms.

American elm seedlings can become established on moist litter, moss, and decayed logs and stumps, but do best on mineral soil. Although they do grow in full sunlight, seedlings perform best with about one-third of full sunlight during the first year. After the first year or two, they grow best in full sunlight. Seedlings that develop in saturated soils are stunted and characterized by early yellowing and loss of the cotyledons, extremely short internodes, and small leaves.

American elm can withstand flooding in the dormant season but dies if the flooding is prolonged into the growing season. Compared with other bottomland species, American elm is intermediately tolerant to complete inundation. Some may be killed by early fall frosts, but those that survive soon are hardened by temperatures alternating between 0° C (32° F) and 10° C (50° F). A constant temperature of 0° C (32° F) for 5 days also hardens the seedlings enough to avoid frost killing *(7)*.

Studies in Iowa and southeastern Michigan on wet lowland and upland mesic sites show that despite high mortality from Dutch elm disease, the next generation will be much like the last. Although American elm has been essentially eliminated from the overstory, it is a significant part of the understory and seedling layers. Some observations suggest that there will be a shift toward more intolerant species under the dead elms. American elm may be perpetuated for generations, even though the average life span of the trees is likely to be reduced. Where seeds are available, American elm is a prominent early invader of abandoned fields. On upland sites in the Midwest, fire, as a natural component of the environment, has kept American elm from invading the prairies *(1,2,12,13)*.

In determining vegetational patterns and succession, allelopathy is apparently not as important for species coming in under American elm as it is for species coming in under sycamore, hackberry, northern red oak, and white oak. In a test in Missouri, there was lower productivity and higher percent soil moisture under all test species but American elm. This apparently was due to toxic leaf leachate present from the four test species, but not present in leachate from American elm *(11)*.

Vegetative Reproduction—Small American elm trees produce vigorous stump sprouts. Although not documented, some observations suggest that replacement in dense, undisturbed bottom-land stands in Minnesota may be by root suckers of mature trees.

American elm can be propagated by softwood cuttings taken in June and treated with indolebutyric acid or by leaf bud cuttings. In a test, greenhouse-grown stock rooted easier than field-grown stock. Propagation by dormant root cuttings has not been effective.

Sapling and Pole Stages to Maturity

Growth and Yield—American elm seldom grows in pure stands and there is no information on stand yields. On good sites in dense forest stands, American elm may reach 30 to 38 m (98 to 125 ft) in height and 122 to 152 cm (48 to 60 in) in d.b.h., with a 15 m (49 ft) clear bole. On medium sites, heights of 24 m (80 ft) are common. On very wet soils or on the very dry soils of the Plains, however, the species is often only 12 to 18 m (40 to 60 ft) tall at maturity. In open-grown or sparse stands, the trees usually fork near the ground and form wide arching crowns. American elm is a long-lived species, often reaching 175 to 200 years, with some older than 300 years.

Rooting Habit—The depth of rooting varies with soil texture and soil moisture. In heavy, wet soils the root system is widespread and within 0.9 to 1.2 m (3 to 4 ft) of the surface. On drier medium-textured soils, the roots usually penetrate 1.5 to 3.0 m (5 to 10 ft). In deep, relatively dry sands in the Dakotas, American elm may develop a taproot reaching 5.5 to 6.1 m (18 to 20 ft) down to the water table.

Reaction to Competition—American elm is classed as intermediate in shade tolerance among the eastern hardwoods. Usually it responds well to release, often growing more rapidly than its associates at advanced ages. Once it becomes dominant in a mixed hardwood stand, it is seldom overtaken by other species. It can persist in the understory of pioneer species such as eastern cottonwood, black willow, and quaking aspen (*Populus tremuloides*) but dies if suppressed by tolerant sugar maple or American beech (*Fagus grandifolia*).

Damaging Agents—Since 1930, when Dutch elm disease reached the United States in a shipment of elm logs from Europe, it has spread to 41 States from coast to coast. The causal fungus, *Ceratocystis ulmi*, is introduced into the sap stream of twigs or small branches during feeding by the smaller European elm bark beetle, *Scolytus multistriatus*, and the native elm bark beetle, *Hylurgopinus rufipes*. Dutch elm disease is characterized by a gradual wilting and yellowing of the foliage, usually followed by death of the branches and eventually the whole tree (*5,14*).

In addition to Dutch elm disease, several other diseases also are responsible for losses in shade and forest elms. Phloem necrosis, caused by a virus (*Morsus ulmi*) is detected by flagging or browned leaves and butterscotch-colored phloem with a wintergreen odor. It is transmitted by the whitebanded elm leafhopper (*Scaphoideus luteolus*) and through root grafts. Trees usually die within a year after symptoms appear. Verticillium wilt (*Verticillium albo-atrum*) is soil borne and usually enters host plants through the roots. Trees show dieback symptoms similar to Dutch elm disease (*10*). Other diseases include diebacks caused by *Cephalosporium* spp. and *Dothiorella ulmi*; a leaf black spot (*Gnomonia ulmea*); twig blight (*Cytosporina ludibunda*); cankers (*Nectria* spp., *Sphaeropsis ulmicola*, and *Phytophthora inflata*); elm wetwood (*Erwinia nimipressuralis*); and elm mosaic virus (*3,4*). Some of the common wood rot fungi are *Pleurotus ulmarius*, *P. ostreatus*, *Armillaria mellea*, *Ganoderma applanatum*, *Phellinus igniarius*, and numerous species of *Polyporus*.

American elm is attacked by hundreds of insect species including defoliators, bark beetles, borers, leaf rollers, leaf miners, twig girdlers, and sucking insects. The carpenterworm (*Prionoxystus robinae*) bores into the sapwood and degrades the wood. Among the insects that defoliate elm are the spring cankerworm (*Paleacrita vernata*), the forest tent caterpillar (*Malacosoma disstria*), the elm leaf beetle (*Pyrrhalta luteola*), the whitemarked tussock moth (*Orgyia leucostigma*), the elm spanworm (*Ennomos subsignaria*), and many other leaf-eating insects that attack elm and other hardwoods. The elm cockscombgall aphid (*Colopha ulmicola*) forms galls on the leaves but does little damage to the tree. Several scale insects attack elm and may cause damage. Both the elm scurfy scale (*Chionaspis americana*) and the European elm scale (*Gossyparia spuria*) are widely distributed. Among the leafhoppers, the whitebanded elm leafhopper is classed as a serious pest since it is the vector for phloem necrosis (*15*).

Besides insect and disease losses, animal damage, and fire, climatic factors also can have an impact on survival and growth of American elm. Young forest trees may sunscald when exposed by harvesting or thinning operations. Open-grown American elm forks and develops a widespread crown that is susceptible to injury by heavy, wet snows and glaze storms. Of 37 tree species examined after an ice storm in Illinois, American elm ranked fourth in susceptibility to ice damage. In dense stands, such injuries are less severe and are not generally a management problem. Although American elm is shallow rooted in wet soils, it is fairly windfirm because the roots are widespread.

The species is reasonably drought resistant, but prolonged drought reduces growth and may cause death. During the drought of 1934, in the Midwest prairie region, losses of American elm and associated species ran as high as 80 to 90 percent. The 1951-54 drought also caused severe losses in the bottom lands of the South where American elm was more susceptible to drought than the lowland red oaks. Prolonged spring floods may cause death or growth loss. Despite suitable temperatures, in Minnesota bottom lands root elongation does not begin until the spring floods recede and soil aeration increases. On these sites and where trees are planted between street and sidewalk, buttress roots often are a result of inadequate soil aeration.

Fire damage is not a major management problem in the North; however, in southern bottom lands, fall and sometimes early spring fires are extremely damaging. Fires can kill seedling- and sapling-size trees and wound larger trees, thus admitting heart-rot fungi.

Animal damage to American elm, from the sapling stage to maturity, is not a serious problem except for sapsucker injury that degrades the wood.

Special Uses

Before the advent of Dutch elm disease, American elm was prized for its use as a street tree. It was fast growing, hardy, tolerant to stress, and appreciated for its characteristic vaselike crown. Beautiful shaded streets in many cities attested to its popularity.

The wood of American elm is moderately heavy, hard, and stiff. It has interlocked grain and is difficult to split, which is an advantage for its use as hockey sticks and where bending is needed. It is used principally for furniture, hardwood dimension, flooring, construction and mining timbers, and sheet metal work. Some elm wood goes into veneer for making boxes, crates, and baskets, and a small quantity is used for pulp and paper manufacture.

Genetics

The study of genetics in American elm has been primarily directed toward combining resistance to Dutch elm disease with desirable growth characteristics. Only a few selections from American elm look promising at this time. Noteworthy is the "American Liberty" elm, a multiclonal variety selected from second-generation crosses of the most resistant parents. Despite high selection intensity, their resistance is still inferior to resistant cultivars derived from Asian or European sources.

A few horticultural forms have been recognized. These are *Ulmus americana columnaris*, a form with a narrow columnar head, *U. americana ascendens*, with upright branches, and *U. americana pendula*, with long pendulous branches.

Hybridization within the genus *Ulmus* has been aimed primarily at breeding for Dutch elm disease and phloem necrosis resistance. Because of the difficulty of hybridizing American elm, which has a chromosome number twice that of all the other elms (56 versus 28), most of the breeding and selection work does not include American elm. Thousands of attempts to cross the American with the Siberian elm have failed. Reports of successful artificial hybridization and verification of hybridizing American elm with other elms are rare.

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Ulmus crassifolia Nutt. Cedar Elm

Ulmaceae Elm family

John J. Stransky and Sylvia M. Bierschenk

Cedar elm (*Ulmus crassifolia*) grows rapidly to medium or large size in the Southern United States and northeastern Mexico, where it may sometimes be called basket elm, red elm, southern rock elm, or olmo (Spanish). It usually is found on moist, limestone soils along water courses with other bottomland trees, but it also grows on dry limestone hills. The wood is very strong; the lumber is mixed with other southern elm species and sold as rock elm. Its seeds are eaten by several species of birds. Within its range, cedar elm is often planted as an ornamental shade tree. It has the smallest leaves of any native elm and is one of two that flower in the fall.

Habitat

Native Range

Cedar elm (figs. 1, 2) can be found from extreme southwestern Tennessee, Arkansas, and eastern and

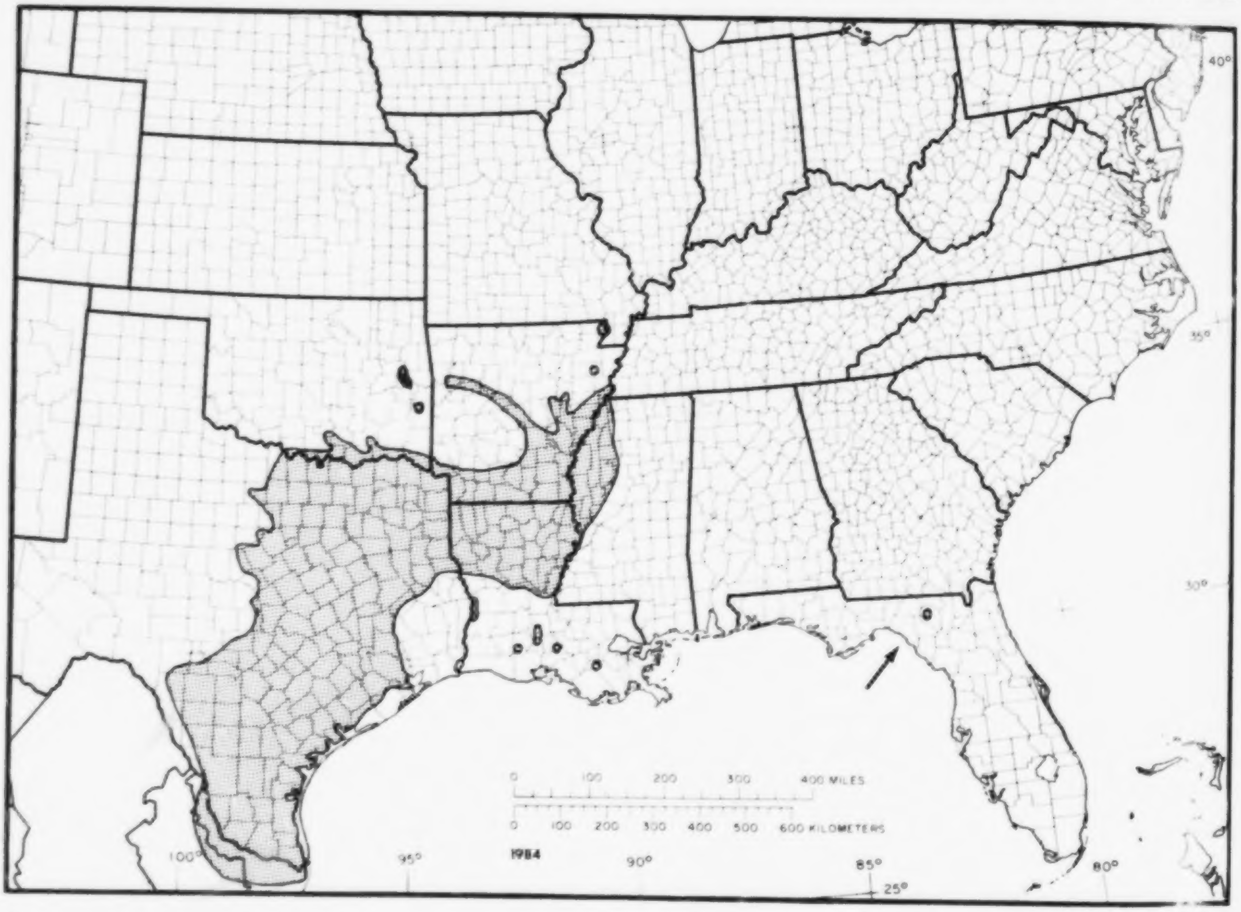

Figure 1—*The native range of cedar elm.*

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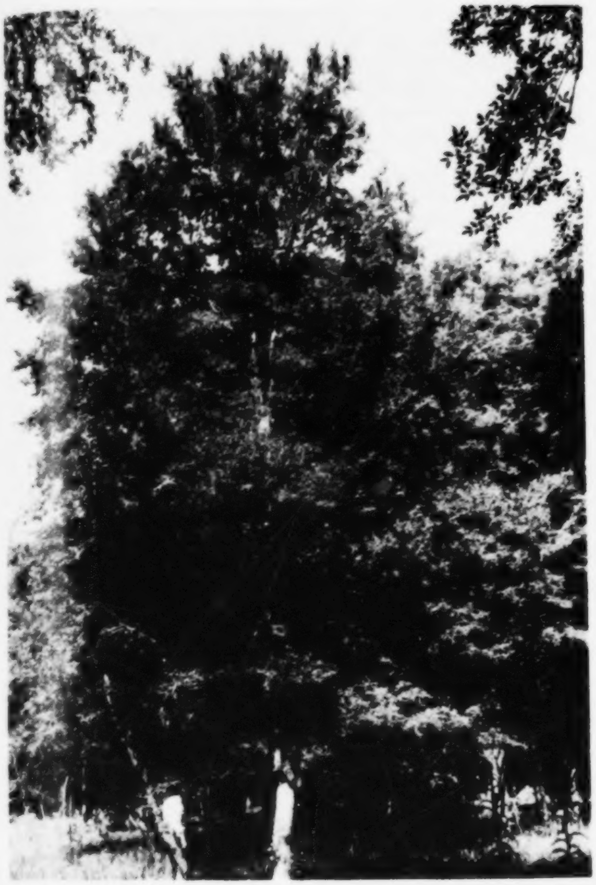

Figure 2—*Cedar elm growing with other bottom-land trees near Apple Springs, Trinity County, TX.*

southern Oklahoma; south to central and southern Texas into the adjacent northeastern Mexican states of Nuevo Leon and Tamaulipas *(15)*; and east to Louisiana and western Mississippi. There is an isolated population in northern Florida *(5,10)*.

Climate

Cedar elm grows mainly in the Gulf Coastal Plain, which has relatively mild temperatures throughout the year. The average January temperature in the region is 8° C (46° F). Oklahoma and Arkansas average 5° C (41° F), while temperatures sometimes reach 17° C (63° F) in southernmost Texas. The average July temperature is 28° C (82° F) *(17)*.

The five main States in which cedar elm is found have an average annual rainfall of 1140 mm (45 in). South Texas averages 460 mm (18 in), while eastern and central Louisiana receive an average annual rainfall of 1470 mm (58 in). The average number of days without a killing frost is 236. All of the States have a minimum growing season of 220 days.

Soils and Topography

Cedar elm thrives in deep rich soils (Inceptisols) in the Mississippi Delta and along streams in Arkansas, Louisiana, Oklahoma, and Texas, where it becomes a large tree along the Colorado and Brazos Rivers *(2,15)*. Cedar elm grows on dense, poorly drained clay soils (Vertisols) in central Texas. It also can be found on dry limestone hills in Texas and Oklahoma, but the tree is small and scrubby in this environment.

Associated Forest Cover

On dry limestone hills of the central Texas "cedar brakes," cedar elm can be found with Ashe juniper (*Juniperus ashei*), live oak (*Quercus virginiana*), hackberry (*Celtis occidentalis*), Shumard oak (*Quercus shumardii*), Mohr oak (*Q. mohriana*), and Durand oak (*Q. durandii*). On the floodplains of major rivers, cedar elm is a minor component of the following forest cover types *(6)*: Sweetgum–Willow Oak (Society of American Foresters Type 92), Sugarberry–American Elm–Green Ash (Type 93) and Overcup Oak–Water Hickory (Type 96).

In addition, a variant of Cedar Elm–Water Oak–Willow Oak (Type 92) is found on low, indistinct or flattened first bottom ridges with poorly drained soils. The variant is also of minor importance on some impervious terrace sites, amounting to high shallow flats.

Other common associates are pecan (*Carya illinoensis*), eastern cottonwood (*Populus deltoides*), red maple (*Acer rubrum*), waterlocust (*Gleditsia aquatica*), honeylocust (*G. triacanthos*), persimmon (*Diospyros virginiana*), laurel oak (*Quercus laurifolia*), water oak (*Q. nigra*), winged elm (*Ulmus alata*), blackgum (*Nyssa sylvatica*), boxelder (*Acer negundo*), and (rarely) baldcypress (*Taxodium distichum*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Cedar elm flowers from August to September and fruit ripens from September to October *(19)*. However, flowering dates have been reported as early as July and fruiting as late as November *(20)*. When flowers appear in

August, fruit ripens in September, and then a second flowering and fruiting may occur in October and November, respectively *(15)*.

Flowers are in fascicles of three to five on slender, pubescent pedicels 8 to 13 mm (0.31 to 0.51 in) long, located in the axils of the leaves. The hairy, red-to-green calyx is divided beyond the middle into four to eight equal and acute lobes, and the stamen is composed of five or six slender filaments and reddish purple anthers. Flowers are perfect *(19)*.

Seed Production and Dissemination—The green fruit, or samara, is oblong and flattened, deeply notched at the apex, 6 to 13 mm (0.25 to 0.5 in) long, and pubescent, especially along the margins. The seed within is unsymmetrical, acute, and covered with a dark chestnut-brown coat. Cleaned seeds average 147,700/kg (67,000/lb). Dissemination is by wind and germination occurs the following spring.

Seedling Development—Air-dried seeds may be stored at 4° C (39° F) for at least 1 year. Stratification at 5° C (41° F) for 60 to 90 days before sowing can improve germination. The seeds should be covered with soil about 5 mm (0.2 in) deep. Germination is epigeal. Approximately 5 to 12 percent of the viable seed produce plantable stock *(19)*. The seedlings can usually be outplanted after one growing season in the nursery.

Vegetative Reproduction—Cedar elm is commonly grown from seed. Though no reference is made to species in the literature, cedar elm can probably be propagated vegetatively like other elms by layering, air-layering, and from greenwood cuttings.

Sapling and Pole Stages to Maturity

Growth and Yield—Cedar elm is classified as a medium to large tree. Reports of height at maturity range from 6 m (20 ft) in the Edwards Plateau of Texas to near 30 m (98 ft) *(2,4)*. The national champion big tree from Limestone County, TX, is 28.7 m (94 ft) tall. Mature trees average approximately 90 cm (36 in) in d.b.h.

Cedar elm has an unusual cross-section that may be triangular, almost square, or deeply irregularly scalloped. The annual growth rings are very indistinct. Thus there may be considerable error in estimating the average growth rate *(3)*. In the early 1950's the Southern Forest Experiment Station estimated a volume of about 5.7 million m^3 (1 billion fbm) in the total United States area *(4)*.

Rooting Habit—The tree is relatively shallow rooted in early life. It is resistant to root pruning in the nursery. In later life the trees are moderately tolerant of soil compaction or disturbance of the root systems *(21)*.

Reaction to Competition—The literature contains no information on tolerance of cedar elm to vegetative competition or tolerance to shade, drought, or other physiological stresses. Observation of seedlings and of crown class, however, strongly suggests that cedar elm should be classed as intermediate in tolerance to shade.

Damaging Agents—Cedar elm is susceptible to the Dutch elm disease caused by the fungus *Ceratocystis ulmi*, which is carried chiefly by the native elm bark beetle *(Hylurgopinus rufipes)* and also by the smaller European elm bark beetle *(Scolytus multistriatus)*. The disease does not seem to be as harmful to cedar elm as to the American elm *(Ulmus americana)*. The offspring of *U. crassifolia* × *parvifolia* crosses indicated an apparent increase in disease resistance *(14)*.

A vascular wilt easily confused with Dutch elm disease and harmful to cedar elm is caused by *Ceratocystis ulmi*. Again, cedar elm is not as susceptible to the disease as is American elm. In Mississippi, only 8.5 percent of 25 large trees 18 cm (7 in) in d.b.h. and larger and 1 percent of 132 small trees 15 cm (6 in) in d.b.h. and smaller were affected by the disease, as opposed to 37 percent of the large and 5.7 percent of the small American elms *(8)*.

Cedar elm also has been found fairly resistant to Texas root rot *(Phymatotrichum omnivorum) (9)*, but only slightly resistant or nonresistant to heartwood decay caused by several species of *Fomes* and *Polyporus (18)*. The symptoms of elm phloem necrosis caused by the mycoplasmalike organism *Morsus ulmi* have been suppressed in American and cedar elm by injections of tetracycline antibiotic *(7)*.

In Texas, Spanish moss *(Tillandsia usneoides)* frequently drapes the branches of cedar elm; it weakens the branches and may kill the tree *(15)*.

The elm leaf beetle *(Pyrrhalta luteola)* is hosted by all species of elm throughout the United States, but it causes only occasional, slight damage to cedar elm *(1)*.

Special Uses

The seeds are part of the diet of several bird species. In south Texas, 10 percent of the diet of the plain chachalaca consists of cedar elm seeds *(11)*. Wild turkey in Texas use elm seeds and buds for 5

to 10 percent of their diet *(12)*. In addition, squirrels eat the buds.

Cedar elm is frequently planted as an ornamental shade tree in Oklahoma and Texas *(21)*.

Cedar elm flowers about the same time as the ragweeds and is known to cause or to complicate later summer hayfever *(5)*.

The wood is known for its great strength and exceptionally good shock resistance. Its specific gravity and shrinkage are quite similar to those of rock elm *(Ulmus thomasii) (4)*. Because their wood is anatomically similar, cedar elm, rock elm, winged elm, and September elm *(U. serotina)* are all classified as "rock elm." They are most easily distinguished by differences in the ultraviolet fluorescence of the aqueous extracts of the heartwood *(16)*.

Because of its similarity to rock elm, cedar elm can be used as a substitute for rock elm *(4)*. It is most suitable for the manufacturing of furniture and fence posts. The wood also is excellent for steam bending and therefore is used to make containers such as boxes, baskets, crates, and barrels. Other products made from the wood include caskets and dairy, poultry, and apiary supplies.

Cedar elm leaves can be used as indicators of the severity of air pollution. The sulfate content of leaf samples shows the long-term exposure to sulfur dioxide, which is related to overall pollution levels *(13)*.

Genetics

Open pollinated hybrids between Chinese elm *(Ulmus parvifolia)* and cedar elm *(U. crassifolia)* have been recorded *(14)*.

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Ulmus rubra Muhl. Slippery Elm

Ulmaceae Elm family

John H. Cooley and J. W. Van Sambeek

Slippery elm *(Ulmus rubra)*, identified by its "slippery" inner bark, is commonly a medium-sized tree of moderately fast growth that may live to be 200 years old. Sometimes called red elm, gray elm, or soft elm, this tree grows best and may reach 40 m (132 ft) on moist, rich soils of lower slopes and flood plains, although it may also grow on dry hillsides with limestone soils. It is abundant and associated with many other hardwood trees in its wide range. Slippery elm is not an important lumber tree; the hard strong wood is considered inferior to American elm even though they are often mixed and sold together as soft elm. The tree is browsed by wildlife and the seeds are a minor source of food. It has long been cultivated but succumbs to Dutch elm disease.

Habitat

Native Range

Slippery elm (fig. 1) extends from southwestern Maine west to New York, extreme southern Quebec, southern Ontario, northern Michigan, central Minnesota, and eastern North Dakota; south to eastern South Dakota, central Nebraska, southwestern Oklahoma, and central Texas; then east to northwestern Florida and Georgia. Slippery elm is uncommon in that part of its range lying south to Kentucky and is most abundant in the southern part of the Lake States and in the cornbelt of the Midwest *(8)*.

Climate

Annual precipitation generally increases from northwest to southeast across the range of slippery elm *(11)*. It averages about 530 mm (21 in) along the North Dakota–Minnesota boundary and about 2110 mm (83 in) at higher elevations in North Carolina. Warm season precipitation ranges from 410 to 1040 mm (16 to 41 in), and snowfall from very rare in the South to 254 cm (100 in) or more in the North. Average annual temperature ranges from 4° to 21° C (40° to 70° F), average January temperature from -15° to 12° C (5° to 54° F), and average July temperature from 16° to 27° C (60° to 80° F). The length of the frost-free period ranges from 90 to 280 days.

Soils and Topography

Slippery elm grows in soils common to the orders Mollisols and Alfisols. It grows best on moist, rich soils of lower slopes, streambanks, river terraces, and bottom land but it is often found on much drier sites, particularly those of limestone origin *(11)*. Examples of sites on which it is, or has been, an important species are flood plains, terraces, and well-drained uplands in east-central Illinois; the northern Mississippi River flood plain; alluvial terraces in western Pennsylvania; and bottom land, lower ravine slopes, and upland in central New York. Slippery elm, along with black cherry *(Prunus serotina)* and red maple *(Acer rubrum)* are frequent invaders of tree plantings following surface-mining *(12)*.

Slippery elm can persist on poorly drained soils that are occasionally flooded for periods of 2 or 3 months but it does not reproduce or grow well if flooding is frequent or prolonged. In Illinois, on the flood plain of the Embarrass River, which is usually flooded at least once each year but not for more than 5 days at a time, slippery elm is most abundant along the river levee and at the edge of the flood plain where there is least chance of prolonged flooding. In another streamside forest, slippery elm was classified as an important subdominant in parts that were not flooded more than 1 percent of the time. In one prairie grove remnant, slippery elm was most important in terms of size and abundance on soils of the Argiudoll group, somewhat less important on Hapludalfs, and least important on Haplaquolls. On the northern Mississippi flood plain, slippery elm is found on the better drained sites; in the upland forest of southern Wisconsin, it is found on the moister sites.

Associated Forest Cover

Slippery elm grows over such a wide range of climatic, soil, and topographic conditions that its associates include more than 60 deciduous tree species. It is a common associate in the forest cover types Black Oak–American Elm–Red Maple (Society of American Foresters Type 39), Hawthorn (Type 109), White Oak–Black Oak– Northern Red Oak (Type 52), and River Birch–Sycamore (Type 61) *(5)*. It probably also appears in Silver Maple–American Elm (Type

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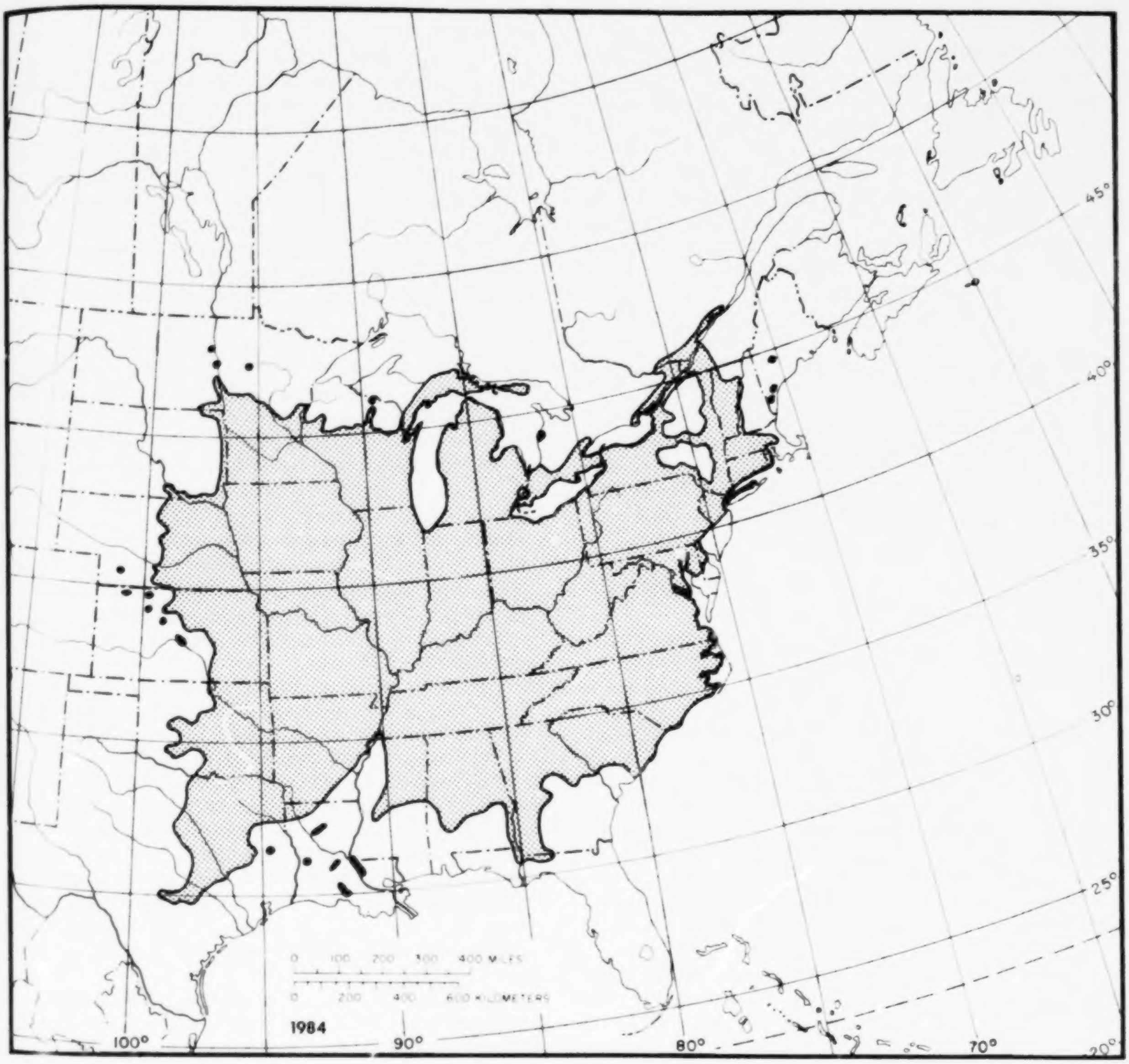

Figure 1—*The native range of slippery elm.*

62) and as an occasional tree in several other cover types. Common associates in uplands include bur, chinkapin, white, black, and northern red oaks (*Quercus macrocarpa, Q. muehlenbergii, Q. alba, Q. velutina,* and *Q. rubra*); shagbark, bitternut, mockernut, and pignut hickories (*Carya ovata, C. cordiformis, C. tomentosa,* and *C. glabra*); sugar, red, and silver maples (*Acer saccharum, A. rubrum,* and *A. saccharinum*); boxelder (*A. negundo*); white ash (*Fraxinus americana*); American elm (*Ulmus americana*); blackgum (*Nyssa sylvatica*); basswood (*Tilia americana*); black cherry; black walnut (*Juglans nigra*); hackberry (*Celtis occidentalis*); and honeylocust (*Gleditsia triacanthos*). On periodically

flooded lowlands slippery elm commonly occurs with silver and red maple, American elm, eastern cottonwood *(Populus deltoides)*, sycamore *(Platanus occidentalis)*, hackberry, blackgum, and honeylocust.

Common understory species of slippery elm stands include blackberry *(Rubus allegheniensis)*; black raspberry *(R. occidentalis)*; prickly, hairystem, and Missouri gooseberries *(Ribes cynosbati, R. hirtellum*, and *R. missouriense)*; roundleaf, alternate-leaf, red-osier, gray, and flowering dogwoods *(Cornus rugosa, C. alternifolia, C. stolonifera, C. racemosa*, and *C. florida)*; beaked hazel *(Corylus cornuta)*; American hazelnut *(C. americana)*; Atlantic leatherwood *(Dirca palustris)*; ninebark *(Physocarpus* spp.); climbing bittersweet *(Celastrus scandens)*; Virginia creeper *(Parthenocissus quinquefolia)*; grape *(Vitis* spp.); American and redberry elders *(Sambucus canadensis* and *S. pubens)*; nannyberry *(Viburnum lentago)*; blackhaw *(V. prunifolium)*; witch-hazel *(Hamamelis virginiana)*; poison-ivy *(Toxicodendron radicans)*; American bladdernut *(Staphylea trifolia)*; coralberry *(Symphoricarpos orbiculatus)*; wild hydrangea *(Hydrangea arborescens)*; eastern burningbush *(Euonymus atropurpureus)*; and trailing wahoo *(E. obovatus) (4,11)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Slippery elm has inconspicuous, perfect flowers that appear in the spring before the leaves, from February to May, depending on weather and location. Seeds ripen from April to June and are dispersed by wind as soon as they are ripe. Large crops are borne every 2 to 4 years, beginning after age 15 *(2)*.

Seed Production and Dissemination—Seeds of slippery elm are larger than many of the native elms. They range from 77,200 to 119,000/kg (35,000 to 54,000/lb) and average 90,400/kg (41,000/lb). Dispersal is by gravity and wind *(2)*.

Seedling Development—Seeds sometimes show dormancy and seedlings are susceptible to damping off. Germination is epigeal *(2)*. Seedlings become established under a wide variety of conditions. Mineral soil seedbeds are best but seeds germinate and survive in forest litter or among grasses and other herbaceous plants. In southeastern Minnesota woodlots the species reproduces more successfully than any other except aspen *(Populus* spp.) and paper birch *(Betula papyrifera)*. In Ogle County, IL, it was the third most important tree species on abandoned pastureland. On gravel bars along the Jacks Fork and Current Rivers in Missouri, slippery elm does not become an important stand component until the bars have already been invaded by pioneer species such as water-willow *(Justica* spp.), Coastal Plain willow *(Salix caroliniana)*, and eastern cottonwood.

Juvenile growth of slippery elm is rapid in the open or under light shade and slightly exceeds that of American elm. In southeastern Minnesota, trees 2.5 cm (1 in) in diameter were 7 to 18 years old, depending on severity of competition.

Vegetative Reproduction—Slippery elm sprouts readily from stumps. During its seedling stage it produces sprouts from rhizomes that sometimes form reproduction less than 0.6 m (2 ft) tall in patches 9.1 m (30 ft) or more in diameter. Roots can be formed in 1 year by layering. Rootstocks of slippery elm are often used to propagate hybrid elms.

Sapling and Pole Stages to Maturity

Growth and Yield—The height growth of slippery elm is most rapid in trees 20 cm (8 in) or less in d.b.h. In a streamside forest in Illinois, slippery elm increased 10 mm (0.4 in) in d.b.h. from 25 cm (9.7 in) to 26 cm (10.1 in) in 11 years. In a stand in Polk County, WI, suppressed and intermediate trees grew 11 mm (0.43 in) while codominant and dominant trees grew 2.9 cm (1.14 in) in 8 years.

On average sites, slippery elm reaches 18.3 to 21.3 m (60 to 70 ft) in height and 61 to 91 cm (24 to 36 in) in d.b.h. On the best sites individuals may reach 41.1 m (135 ft) in height and 122 cm (48 in) in d.b.h. The largest living specimen, located in Perry County, PA, is 27.4 m (90 ft) tall and 193 cm (76 in) in d.b.h.

Reaction to Competition—On sites to which it is well adapted, slippery elm is one of the more shade-tolerant species. It is much more tolerant than quaking aspen but slightly less tolerant than sugar maple. Reproduction is erratic under fully stocked stands. In a river terrace forest in east-central Illinois, slippery elm was present in most size classes but there were no seedlings, whereas a nearby upland coppice stand contained numerous slippery elm seedlings. It is most frequently a component of the subcanopy. Overall, it is classed as tolerant of shade.

Damaging Agents—Excluding insect species that feed only on American elm, more than 125 insect species feed on trees in the elm genus *(1)*. Bark beetles and wood borers generally cause little damage to vigorous trees although some can ultimately kill weakened or diseased trees. They also introduce stain and rot organisms into dead trees and manufactured products. The spread of Dutch elm disease is the most detrimental effect of bark beetle feeding. The smaller European elm bark beetle (*Scolytus multistriatus*) is the primary vector of this disease in the United States, but the native elm bark beetle (*Hylurgopinus rufipes*, *Scolytus mali*, and *Xylosandrus germanus*) are also able to transmit it.

Only a few defoliators feed exclusively on elms and even fewer feed exclusively on slippery elm. The elm calligrapha (*Calligrapha scalaris*), the elm leaf beetle (*Pyrrhalta luteola*), the larger elm leaf beetle (*Monocesta coryli*), *Canarsia ulmiarrosorella*, an elm casebearer (*Coleophora ulmifoliella*), *Nerice bidentata*, and one species of the genus *Macroxyela* usually feed only on elms. Slippery elm is especially favored by the larger elm leaf beetle. Elms are preferred hosts for *Dasychira basiflava*, fall cankerworm (*Alsophila pometaria*), spring cankerworm (*Paleacrita vernata*), whitemarked tussock moth (*Orgyia leucostigma*), the yellownecked caterpillar (*Datana ministra*), and the elm sawfly (*Cimbex americana*). Although larvae of the gypsy moth (*Lymantria dispar*) will feed on leaves of slippery elm, it is not a preferred host.

Sucking insects that feed exclusively on elm or prefer elm to most other species include elm cockscombgall aphid (*Colopha ulmicola*), *Tetraneura ulmi*, European elm scale (*Gossyparia spuria*), elm scurfy scale (*Chionaspis americana*), elm leaf aphid (*Tinocallis ulmifolii*), woolly apple aphid (*Eriosoma lanigerum*), and woolly elm bark aphid (*E. rileyi*). The gall aphid (*Kaltenbachiella ulmifusa*) is limited to slippery elm. The whitebanded elm leafhopper (*Scaphoideus luteolus*) is the principal vector of elm phloem necrosis.

Slippery elm has many of the same diseases as American elm (*6*). It is attacked and killed by Dutch elm disease caused by the fungus *Ceratocystis ulmi*. It is also killed by elm yellows or elm phloem necrosis (a mycoplasma-like organism) throughout much of its range. These two diseases are so virulent and widespread that slippery elm seldom reaches commercial size and volume as a forest tree and it is being replaced as a street tree in many localities. A dieback caused by *Dothiorella ulmi* is widespread from New England to Mississippi and has often been confused with Dutch elm disease. A leaf spot caused by *Gnomonia ulmea*, brown wood rot caused by *Pleurotus ulmarius*, white flakey rot caused by *P. ostreatus*, ustulina butt rot caused by *Ustulina vulgaris*, slimeflux and wetwood caused by *Erwinia nimipressuralis*, and nectria canker caused by *Nectria galligena* all attack slippery elm. In a survey in Davidson County, TN, infestations of mistletoe (*Phoradendron flavescens*) were more numerous on slippery elm than on any other species except American elm and white ash.

Slippery elm is also damaged by several other agents. In mixed hardwood stands, bark stripping by deer is more frequent on slippery elm than on other species. Bark stripping occurred most frequently on stems of saplings and on roots of pole-sized trees (*9*). Slippery elm also suffers crown breakage following severe ice storms in Wisconsin (*3*).

Special Uses

Slippery elm wood, although considered inferior to American elm, is used commercially for the same products: furniture, paneling, and containers. The seeds are eaten by birds and small animals. Deer and rabbits browse the twigs.

Genetics

Morphological observations that the *Ulmus* genera is composed of two distinct groups were confirmed with analyses of leaf flavonoids (*13*). Slippery and American elm, the unwinged species, produce kaempferol and quercetin, while the winged species produce myrictein. No studies of genetic diversity have been reported for slippery elm.

Because this species is so widely distributed, ecotypes and races probably exist. Like those of most elm species, vegetative cells of naturally growing slippery elm contain 28 chromosomes (14 pairs) and there are no genetic barriers to gene exchange among diploid elm species (*10*). Slippery elm is commonly crossed with Siberian elm (*Ulmus pumila*). The F_1 hybrids tend to have morphological characteristics intermediate between parents and grow faster than Siberian elm but the susceptibility of these hybrids, as well as three species combined with Japanese elm (*U. japonica*), to Dutch elm disease is a function of the proportion of slippery elm genes present (*7*). Pollination of Chinese elm (*U. parvifolia*) and September elm (*U. serotina*) with slippery elm pollen have produced hybrid seedlings.

Natural hybrids of rock elm and slippery elm have been observed in Sawyer County, WI, and along streets in Columbia, MO. Ecological isolation probably accounts for the limited occurrence of natural hybrids of these two species (*11*).

A triploid elm has been reported that was determined to be an F_1 seedling of Siberian elm × slippery elm.

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Ulmus serotina Sarg. September Elm

Ulmaceae Elm family

Edwin R. Lawson

September elm (*Ulmus serotina*), also called red elm, is one of two fall-flowering native elms. This medium-sized, rapid-growing tree is found most frequently on moist clay or sandy loam soils, but it also grows on dry, rocky soils of limestone origin. It is never abundant and in early development it is an inconspicuous understory component of hardwood stands. This species may appear more frequently within its range than is currently documented because it may be confused with other elm species. The lumber is cut and sold with four other elm species and marketed as rock elm. Wildlife browse young trees and eat the seeds and buds. September elm is planted in landscapes but succumbs to Dutch elm disease.

Habitat

Native Range

September elm (fig. 1) grows sporadically from southern Illinois across Kentucky and Tennessee to

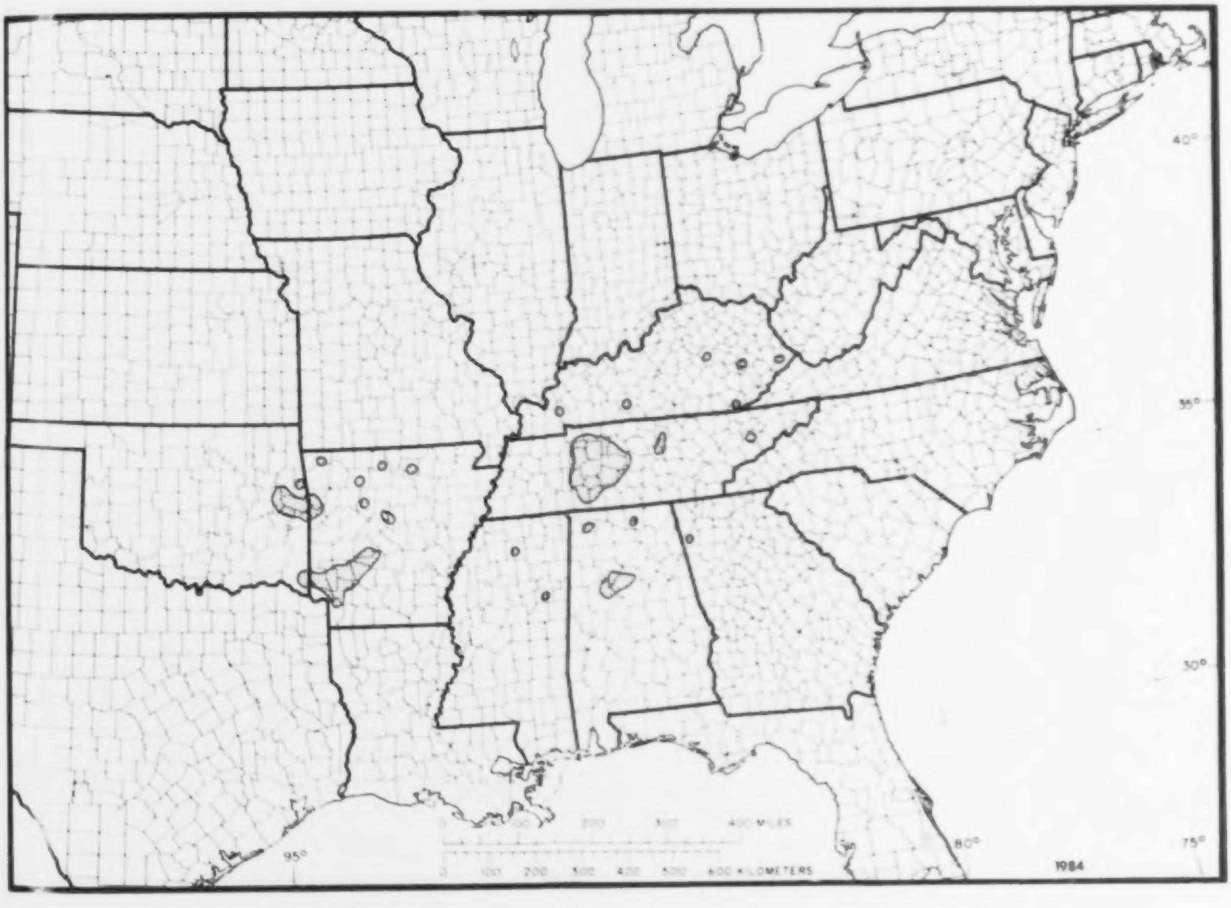

Figure 1—*The native range of September elm.*

The author is Professor, Department of Forest Resources, University of Arkansas at Monticello.

northern Georgia, northern Alabama, northern Mississippi, Arkansas, and eastern Oklahoma *(5)*. It is most abundant in Arkansas and Tennessee.

Climate

The distribution of September elm is in the humid to temperate zones of the East-Central United States. Average annual precipitation ranges from about 1020 mm (40 in) to about 1320 mm (52 in), of which about 50 to 65 percent occurs from April through September. Average annual snowfall over the region ranges from about 5 cm (2 in) to 50 cm (20 in). Average annual temperatures range between 13° C (55° F) and 17° C (62° F), but the lowest and highest temperatures observed are -23° C (-10° F) and 46° C (115° F), respectively. The growing season averages between 180 and 220 days over the species range *(15)*.

Soils and Topography

September elm grows most frequently on moderately to well-drained, moist soils varying in texture from clay loams to sandy loams. It is also common on dry, rocky soils derived from limestone or other calcarous material. It is less frequent on alluvial soils along streams in rich bottoms and on the margins of swamps *(4,12)*. The clay loams and sandy loams are principally in the order Ultisols and suborder Udults. The Udults are usually moist, with relatively low amounts of organic matter in the subsurface horizons. They are formed in humid climates that have relatively short or no dry periods during the year. September elm is reported in some localities where Alfisols and Inceptisols are present. Alfisols are medium to high in bases and have gray to brown surface horizons and clay accumulations in subsurface horizons. They are usually moist but may be dry during summer. Inceptisols have weakly differentiated horizons, with materials that have been altered or removed, but have not accumulated. These soils are also moist but may be dry during the warm season *(17)*.

September elm grows at elevations ranging from about 100 m (325 ft) in the more southerly part of its range to about 460 m (1,500 ft) in northerly areas. Sites vary from very flat topography to moderate slopes in some of the upland coves and ravines. It has been reported to grow in upland coves and ravines in Arkansas *(14)* but is notably absent from the poorly drained lowlands of the Mississippi alluvial plain *(12)*.

Associated Forest Cover

September elm is generally very scattered, and there are few records of stands with this species as a primary component. It is not a common associate in any of the forest cover types currently listed by the Society of American Foresters.

September elm often grows on floodplains in mid- to late-successional communities where common associates are American elm *(Ulmus americana)*, river birch *(Betula nigra)*, sweetgum *(Liquidambar styraciflua)*, and sometimes silver maple *(Acer saccharinum)*. In coves and on mesic slopes it may grow with American hornbeam *(Carpinus caroliniana)*, Florida maple *(Acer barbatum)*, white ash *(Fraxinus americana)*, blue ash *(F. quadrangulata)*, sweetgum, northern red oak *(Quercus rubra)*, white oak *(Q. alba)*, and American elm. Its common appearance on streamsides, roadsides, and other openings may indicate low shade tolerance *(13)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—September elm and cedar elm *(Ulmus crassifolia)* are the two species of native elms that flower and bear fruit in the fall. The hermaphroditic, protogynous flowers of September elm usually appear in September and are in small racemes in the leaf axils of the current season *(2)*. The fruit are light-greenish samaras that turn brown as they ripen in late October or early November. The winged fruits are 10 to 13 mm (0.4 to 0.5 in) long, oblong-elliptical in shape, deeply divided at the apex and fringed along the margins with white hairs *(11)*.

Seed Production and Dissemination—Most species of elm produce good seed crops every 2 or 3 years, but seed production data for September elm are not available. The seeds are dispersed by gravity and wind. Cleaned seeds are very small, averaging about 328,500 per kilogram (149,000/lb) *(1)*.

Seedling Development—Naturally dispersed seeds overwinter in the litter or at the soil surface and germinate the following spring. Germination is epigeal *(1)*. If seeds are to be sown in a nursery, they should be stratified at 5° C (41° F) for 60 to 90 days *(1)*. Nursery-grown seedlings are usually outplanted as 1–0 stock.

Vegetative Reproduction—September elm, like many other elms, sprouts readily when the stem is severed or badly injured. Damaged young trees sprout more readily than older trees, and sprouts grow rapidly.

Sapling and Pole Stages to Maturity

Growth and Yield—September elm grows rapidly on good sites with low competition. Trees attain a diameter of 60 cm (24 in) to 90 cm (36 in) *(4)* and may reach a height of 25 m (82 ft). The tree attains the general form of American elm, but branches are smaller and somewhat more pendulous. Lower portions of large trees may provide logs of veneer quality.

Rooting Habit—No information available.

Reaction to Competition—September elm is classed as tolerant of shade and probably exists most commonly as an inconspicuous understory plant during early developmental stages. Upon release, growth response is rapid, especially on better sites. If competition is minimal, however, the species will grow rapidly during all stages of development.

Damaging Agents—The susceptibility of September elm to Dutch elm disease *(Ceratocystis ulmi)* is probably the greatest deterrent to its growth and development. All three mature specimens of September elm at the National Arboretum have been killed by this fungus since 1965; seedlings of the species are also very susceptible to Dutch elm disease *(9)*.

September elm has also been reported as a host of American mistletoe, *Phoradendron flavescens (6)*.

Special Uses

The seeds of September and other elms are eaten by a variety of birds and small mammals, including squirrels. Twigs and buds are sometimes browsed by deer, and a few game birds eat the buds *(3)*.

The species has been planted as an ornamental tree in Georgia and Alabama, where it grows abundantly in hilly areas *(11)*. This elm is also reported to thrive in Massachusetts *(10)*.

The reddish-brown wood of September elm is hard, close grained, and very strong and can be polished to a high luster. It is one of four species included as "rock elm" in commercial lumbering *(16)*. This group has a specific gravity of 0.57 to 0.63 and moisture contents of 44 and 57 percent for the heartwood and sapwood, respectively. Elm wood also has excellent bending qualities.

Genetics

Little information is available on genetic characteristics of September elm. Santamour *(7)* reported that the chromosome number of September elm was diploid (2n=28) and he later *(8)* used this characteristic to advantage in making crosses of Chinese elm *(Ulmus parvifolia)* and September elm with nine spring flowering species. Fourteen hybrids were developed from these interspecific crossings, four of which were from *U. serotina*. Later crosses of September elm with Siberian elm *(U. pumila)* showed that the hybrids were very susceptible to Dutch elm disease *(9)*.

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Ulmus thomasii Sarg. Rock Elm

Ulmaceae Elm family

T. R. Crow

Rock elm (*Ulmus thomasii*), often called cork elm because of the irregular thick corky wings on older branches, is a medium-sized to large tree that grows best on moist loamy soils in southern Ontario, lower Michigan, and Wisconsin. It may also be found on dry uplands, especially rocky ridges and limestone bluffs. On good sites, rock elm may reach 30 m (100 ft) in height and 300 years of age. It is always associated with other hardwoods and is a valued lumber tree. The extremely hard, tough wood is used in general construction and as a veneer base. Many kinds of wildlife consume the abundant seed crops.

Habitat

Native Range

Rock elm (figs. 1, 2) is most common to the Upper Mississippi Valley and lower Great Lakes region. The native range includes portions of New Hampshire,

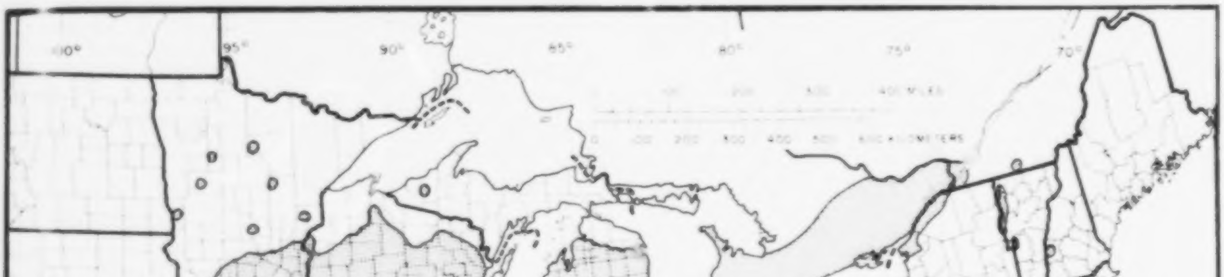

Figure 1—*The native range of rock elm.*

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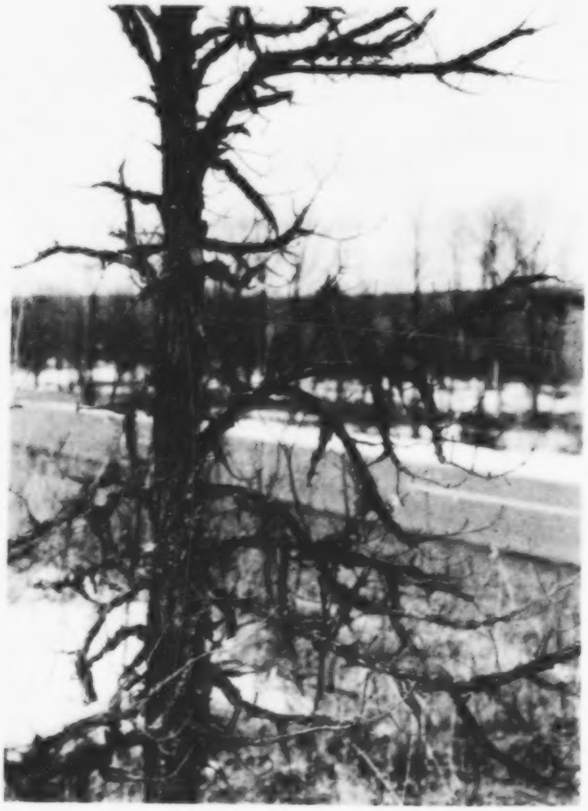

Figure 2—*The presence of conspicuous ridges of corky bark on the branches and older twigs of this 18 cm (7 in) in d.b.h. rock elm is one of its identifying features.*

Vermont, New York, and extreme southern Quebec; west to Ontario, Michigan, northern Minnesota; south to southeastern South Dakota, northeastern Kansas, and northern Arkansas; and east to Tennessee, southwestern Virginia, and southwestern Pennsylvania. Rock elm also grows in northern New Jersey.

Climate

The climatic conditions associated with the distribution of rock elm can be characterized as continental, with cold winters and warm summers. Within the species range, a maximum summer temperature of 38° C (100° F) and a minimum winter temperature of -34° C (-30° F) are common.

Annual precipitation is 640 mm (25 in) in the western part of the range and 1270 mm (50 in) in the extreme southern and eastern parts. At least half of this precipitation occurs during the growing season. Snowfall averages from 50 to 200 cm (20 to 80 in), depending on geographic location.

The frost-free period averages 100 days in the north and 200 days in the south. Rock elm grows best where the frost-free period is from 120 to 160 days.

Soils and Topography

Rock elm is most frequent in lower Michigan, Wisconsin, and southern Ontario, and it is regularly found on moist but well-drained sandy loam, loam, or silt loam soils in mixture with other hardwoods. In Wisconsin, rock elm (fig. 3) is most frequent in the southern wet-mesic forest (7). Although rock elm often grows on rocky ridges, limestone outcroppings, and streambanks, the highest quality sawtimber is found on deeper loamy soils.

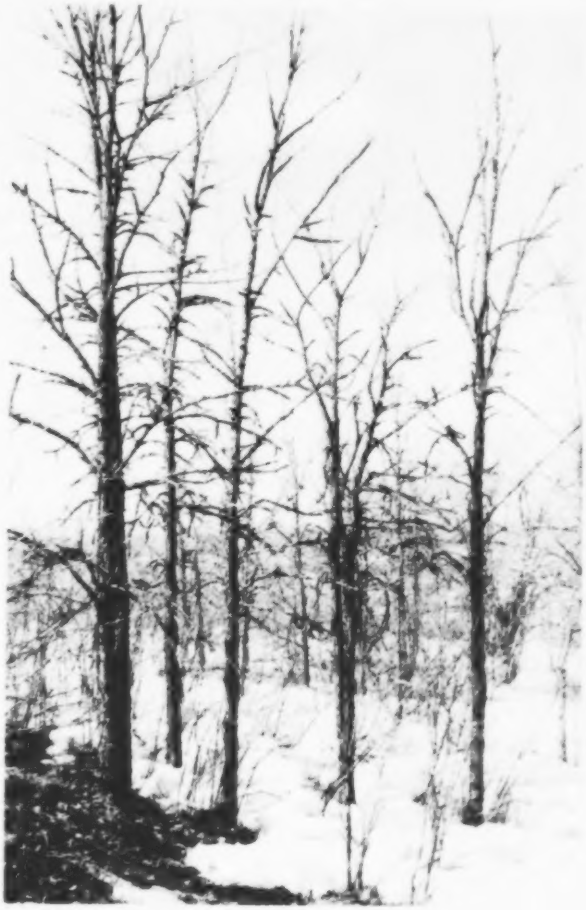

Figure 3—*Rock elm saplings in Wisconsin.*

The major soil orders associated with the distribution of rock elm are the Mollisols, Alfisols, and the Spodosols. Most common are the Hapludalfs (Gray-Brown Podzolic soils) within the Udalfs suborder of the Alfisols. Soil pH ranges from slightly alkaline or neutral to strongly acid.

Associated Forest Cover

Rock elm is a minor component in two forest cover types: Sugar Maple–Beech–Yellow Birch (Society of American Foresters Type 25) and Black Ash–American Elm–Red Maple (Type 39). In addition to type species, other important associates include white ash *(Fraxinus americana)*, black cherry *(Prunus serotina)*, basswood *(Tilia* spp.), northern red oak *(Quercus rubra)*, American elm *(Ulmus americana)*, eastern hophornbeam *(Ostrya virginiana)*, and eastern hemlock *(Tsuga canadensis)*.

Some of the woody shrubs commonly associated with rock elm include prickly ash *(Zanthoxylum americanum)*, beaked hazel *(Corylus cornuta)*, blackberry and raspberry *(Rubus* spp.), dogwoods *(Cornus* spp.), gooseberry *(Ribes* spp.), Atlantic leatherwood *(Dirca palustris)*, bittersweet *(Celastrus scandens)*, Virginia creeper *(Parthenocissus quinquefolia)*, grape *(Vitis* spp.), hawthorn *(Crataegus* spp.), American and redberry elder *(Sambucus canadensis* and *S. pubens)*, and nannyberry *(Viburnum lentago)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Rock elm flowers appear 2 weeks before the leaves at any time from March to May, depending on locality and site. The perfect flowers are protandrous, that is, the male elements of the flower develop 2 to 4 days before the female elements are receptive *(6)*. Female flowers are receptive for only a few days.

The hairy fruit has a broad wing from 13 to 25 mm (0.5 to 1 in) long and matures during May or June. Clean, fully ripened, unwinged seeds number from 11,000 to 19,800/kg (5,000 to 9,000/lb). Seeds germinate soon after they ripen.

Seed Production and Dissemination—Trees 20 years old produce viable seeds, but maximum yields are from trees 45 to 125 years old. Good crops occur every 3 or 4 years. Ripe seeds are dispersed as the leaves become fully expanded, which is usually 2 or 3 weeks later than the time of seed drop for American elm *(9)*.

Although the thin, hair-fringed, winged samaras seem adapted to wind dispersal, seeds are generally carried no more than 40 to 45 m (100 to 150 ft) from the parent tree. The fact that rock elm grows as scattered individuals, often several miles from the nearest seed source, suggests that birds and small mammals play a role in dissemination. The large but very light seeds are also buoyant and water can carry them long distances. As a result, seeds often are concentrated along the banks of streams and lakes.

Seedling Development—Rock elm seeds germinate within a week or two after dispersal if moisture conditions are favorable. In a germination test, 90 to 100 percent of mature seeds were viable *(2)*. Viability was not significantly different between seeds from different trees, between seeds with wings or without wings, or between seeds with seed coats or without seed coats. When germinated in a petri dish, radicles of the viable seeds emerged within 2 or 3 days and were 2.5 to 3.8 cm (1 to 1.5 in) long by the end of the fifth day. Germination is epigeal. The cotyledons began to open about the fifth or sixth day. Under favorable conditions, rock elm seedlings are from 5 to 8 cm (2 to 3 in) tall by the end of the first summer.

Despite its high seed viability, rock elm regenerates poorly *(2,9)*. Germination tests failed when mineral soil and equal volumes of peat moss, sand, and mineral soil were used for planting media, but 70 to 80 percent emergence was obtained in flats using peat moss. Another factor affecting seedling establishment is the persistence of dormant terminal buds. Emergent seedlings rarely develop more than a single pair of true leaves during the first growing season due to this dormancy. Observations on more than 200 seedlings indicated that only 1 percent broke dormancy long enough to develop an additional internode and a second pair of true leaves.

This species appears to be shade tolerant during the seedling stage *(10)*. However, under field conditions with competition, 1.5-0 nursery stock averaged only 27 cm (10.6 in) in height 5 years after planting and only 52 cm (20.4 in) 10 years after planting in northern Wisconsin. In the same study, survival ranged from 85 percent at the end of the 1st year to 32 percent at the end of the 10th year.

Vegetative Reproduction—Rock elm regenerates vegetatively from root suckers and stump sprouts *(10)*, but vegetative reproduction in the field is uncommon.

Most elms are considered difficult to root by means of cuttings. However, leaf-bud cuttings, consisting of leaf blade, axillary bud, and a shield of stem tissue, treated with a growth hormone and held under constant mist on a rooting medium of sand or mica, produced satisfactory results for several species of elm including rock elm *(5)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Few species have rock elm's capacity for recovering from prolonged suppression. An analysis of 153 trees indicated that a large percentage had survived under suppression for 50 years or more. This capacity makes it difficult to correlate diameter and age *(9)*:

D.b.h. class	Crown class			
	Dominant	Codominant	Intermediate	Suppressed
	age in years			
2.5 cm or 1 in	14	22	30	48
7.6 cm or 3 in	26	50	64	99
12.7 cm or 5 in	39	72	97	—
17.8 cm or 7 in	51	93	—	—
22.9 cm or 9 in	63	—	—	—

The average number of rings per 2.5 cm (1 in) of radius by crown class was about 50 for suppressed, 30 to 40 for intermediate, 20 to 30 for codominants, and 10 to 20 for dominants.

On average to better sites, mature rock elm may reach 27 m (90 ft) in total height and 61 cm (24 in) in d.b.h. *(12)*. In virgin hardwood stands in the east and north, 27 to 30 m (90 to 100 ft) heights and 91 to 152 cm (36 to 60 in) in d.b.h. have been recorded *(10)*. Much smaller trees occur along river bluffs, on limestone outcrops, or other sites with thin soil mantles. Rock elm may live 250 to 300 years.

Rooting Habit—No information available.

Reaction to Competition—Rock elm is considered shade tolerant in the seedling-sapling stage and often recovers successfully after long periods of suppression at these stages. As the tree grows older, however, it apparently becomes more light demanding. Overall, the species is classed as intermediate in tolerance to shade *(10)*.

Damaging Agents—Nearly all native North American elm species are susceptible to Dutch elm disease *(Ceratocystis ulmi) (6,13)* and isolates of *C. ulmi* have been obtained from rock elm logs *(5)*. It is likely that Dutch elm disease will greatly reduce the number of rock elm.

A seed-borne fungus *(Gleosporium ulmicolum)* has been reported for rock elm but few of the fungi that are able to invade the fruits and seeds of North American hardwoods are thought to be pathogens that reduce germination or weaken seedlings *(1)*.

Although rock elm has not been listed as a particular host for specific insects, undoubtedly it is host to the various borers, defoliators, and sucking insects that attack American elm.

Throughout the range of rock elm, killing frosts are common during the flowering period and subfreezing temperatures may prevent seed development in some years.

Special Uses

The seeds and buds of rock elm are eaten by deer, rabbits, squirrels, and a variety of birds. Small mammals such as chipmunks, ground squirrels, and mice apparently relish the filbertlike flavor of rock elm seed and frequently eat the major part of the crop.

Rock elm wood has long been valued for its exceptional strength and superior quality *(3,8)*. For this reason rock elm has been drastically overcut in many localities. The wood is stronger, harder, and stiffer than any of the other commercial species of elms. It is highly shock resistant and has excellent bending qualities which make it good for bent parts of furniture, crates and containers, and a base for veneer. Much of the old-growth was exported for ship timbers. Currently, the highest quality sawtimber is found in north-central Wisconsin, lower Michigan, and southeastern Ontario.

Genetics

In a study of compatibility and crossability in *Ulmus (11)*, the form of dichogamy (protandry or protogyny) correlated with the compatibility between the different species. *Ulmus thomasii* is a protandry species and is compatible with two other protandry species—*U. pumila* and *U. laevis*. *Ulmus thomasii* is also self-fertile.

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Umbellularia californica (Hook. & Arn.) Nutt.

California-Laurel

Lauraceae Laurel family

William I. Stein

California-laurel (*Umbellularia californica*) is the most valued and best publicized hardwood species in the Western United States. It is a monotypic, broad-leaved evergreen with many common names, including bay, laurel, California-bay, Oregon-myrtle, myrtlewood, Pacific-myrtle, spice-tree, and pepperwood *(50)*. The names are derived from leaf, fruit, or wood characteristics and also from some similarities often mistaken for relationships with the myrtle and laurel trees of the Mediterranean area *(12,25)*. Decorative items made from the hard, beautifully grained wood are widely marketed as myrtlewood.

Habitat

Native Range

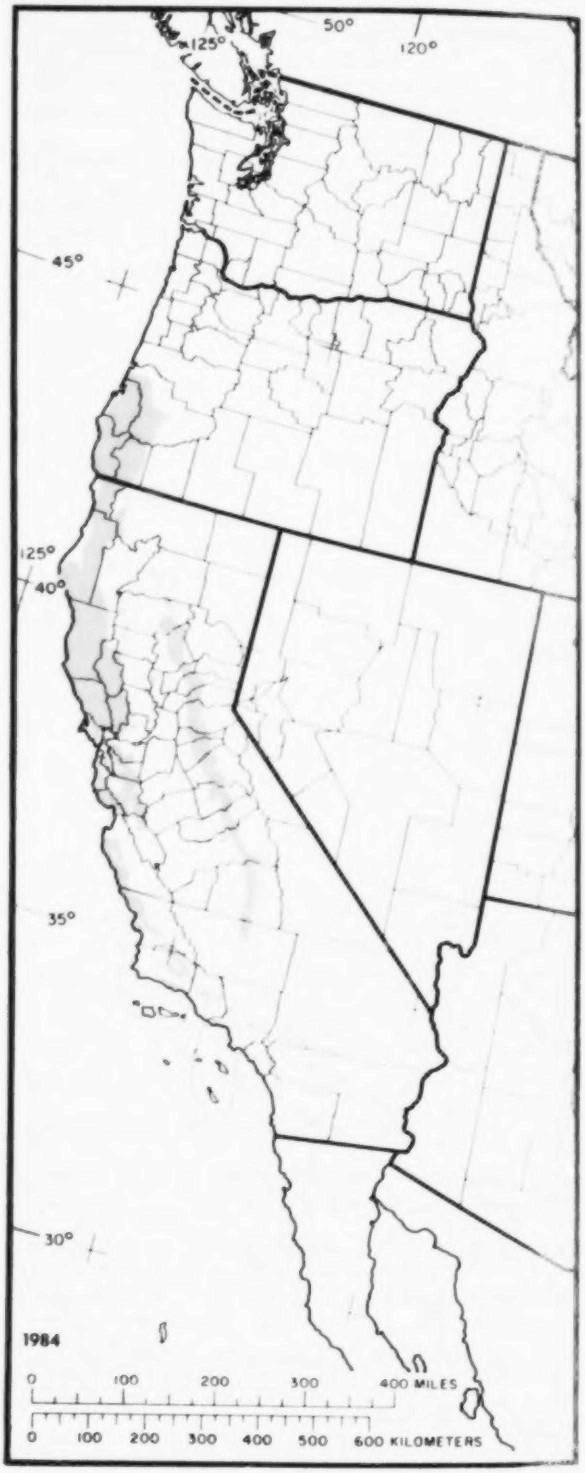

Figure 1—*The native range of California-laurel.*

The range of California-laurel (fig. 1) spans more than 11° of latitude, from below the 44th parallel in the Umpqua River Valley of Douglas County, OR, south beyond the 33d parallel in San Diego County, CA. In the Coast Ranges, the southern limit is on eastern slopes of the Laguna Mountains, a short distance from the Mexican border *(19)*. In the Sierra Nevada, it extends as far south as the west slope of Breckenridge Mountain in Kern County *(58)*. Eastward from the coast, California-laurel extends to the foothills of the Cascade Range in Oregon and California, into the western Sierra Nevada for its entire length, and to the inland side of the Coast Ranges south of San Luis Obispo, CA. Its farthest extent inland, about 257 km (160 mi), is in the southern Sierra Nevada.

Climate

California-laurel grows in diverse climates, ranging from the cool, humid conditions found in dense coastal forests to the hot, dry atmospheres found inland in open woodlands and chaparral. Records from 38 climatic observation stations within or bordering its range indicate that California-laurel has endured temperature extremes of –25° to 48° C (–13° to 118° F) *(41,46,59)*. Average annual temperatures

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range from 8° to 18° C (46° to 64° F); average temperatures in January, from -1° to 10° C (31° to 50° F); and in July, from 13° to 29° C (56° to 84° F).

Average annual precipitation ranges from 338 mm (13.3 in) at Lemon Cove in the southern Sierra Nevada to 2118 mm (83.4 in) at Gold Beach by the mouth of the Rogue River in Oregon. Average annual snowfall ranges from zero at some coastal locations to 742 cm (292 in) at Blue Canyon in Placer County, CA. Average precipitation in the growing season (April through September) ranges from 18 to 432 mm (0.7 to 17.0 in). Length of average frost-free season (above 0° C or 32° F) ranges from 139 to 338 days. Clearly, California-laurel demonstrates broad ecologic versatility.

Soils and Topography

California-laurel grows to tree size in a wide variety of topographic locations and kinds of soil if moisture conditions are favorable. It grows on steep mountain slopes, exposed ridges, coastal bluffs, and rocky outcrops, as well as in protected valleys, alluvial flats, deep canyons and ravines, and low hills. In Oregon and most of California, it grows from sea level to 1220 m (4,000 ft). Near the southern end of the species' range, the lower altitudinal limit rises to 610 m (2,000 ft) on south slopes of the San Bernardino Mountains, and the upper limit approaches 1520 m (5,000 ft) on the west slopes of the San Jacinto Mountains. In the Sierra Nevada, the upper limit reaches 1520 m (5,000 ft) in Kaweah Basin west of Sequoia National Park *(24)*.

Even in dry, hot climates it can become a large tree on moist sites; specimens of unusual height, diameter, crown spread, and age can be found in many California counties *(43)*. Distribution is more restricted in such climates, however, and the species is most common on alluvial deposits or gravelly outwashes at the mouths of canyons, on protected slopes, along and near watercourses, near springs and seeps, and in spring-watered gulches. Under very adverse conditions, California-laurel grows as an understory shrub, as a common component of chaparral, or even as a prostrate mat near the ocean *(24,47)*.

In tree or shrub form, California-laurel grows in soils derived from alluvial deposits, from sedimentary rocks, from volcanic flows of the Cascades and Sierra Nevada, and from old formations in the Klamath and Siskiyou Mountains. It grows on soils of three or more orders; principal among these are Inceptisols, Mollisols, and Ultisols. Specific soils supporting growth of California-laurel include the Ben Lomond, Felton, Gazos–Sweeney, Gazos–Calera, Hugo, Hugo–Josephine, Los Gatos, Los Gatos–Maymen, Maymen, Montara, and Soquel series in the Santa Cruz Mountains *(61)*; the Los Osos adobe clay in the Berkeley Hills *(35)*; alluvium and the Galice, Umpqua, and Tyee sedimentary formations in coastal California and Oregon *(22,62)*; and gabbro, peridotite, and serpentine in the Siskiyou Mountains *(22,63)*. Best development and most rapid growth occur on deep, well-drained alluvial benches and valley bottoms subject to occasional inundation. Growth is also good on well-watered soils of coastal slopes and along higher foothill streams.

The pH of several surface soils supporting pure or mixed stands of California-laurel was found to range from 5.7 to 7.4 *(34,61,62,63)*. Soil properties under California-laurel crowns in central California generally did not differ significantly from those under crowns of the nearest associate species *(61)*.

Associated Forest Cover

California-laurel is more commonly found in mixture with other species than in pure stands. Choice pure stands were eliminated when coastal and inland valleys were cleared for agriculture, and only scattered groves and tracts of large mature trees remain—many in parks or preserves *(40)*. Pure stands of tall young growth are also limited (fig. 2), but pure stands of shorter trees, thickets, or prostrate mats are common on coastal bluffs, in canyons, and elsewhere in California *(19,24,35,61)*.

California-laurel is listed as an associated species in six forest cover types: Port Orford-Cedar (Society of American Foresters Type 231), Redwood (Type 232), Oregon White Oak (Type 233), Douglas-fir–Tanoak–Pacific Madrone (Type 234), Canyon Live Oak (Type 249), and California Coast Live Oak (Type 255) *(13)*. Its prominence in these types, as well as in several others for which it is not specifically listed, varies widely.

Many trees, shrubs, and herbaceous plants are associated with California-laurel in different parts of its extensive range (table 1). The listing in table 1 is not exhaustive; it indicates the variety of associated species. Usually, fewer species and fewer individuals per species are found under the California-laurel canopy than under the canopy of associated trees, and the area bare of all vegetation is greater. In the Coast Ranges south of San Francisco Bay, an average of 36 species per site, mostly perennials, was found under the California-laurel canopy, 55 species beneath the canopy of other trees *(61)*. Distances bare of vegetation along transects ranged from 9 to 48 percent of the total under California-laurel, 0 to 10 percent under other trees. Where the laurel

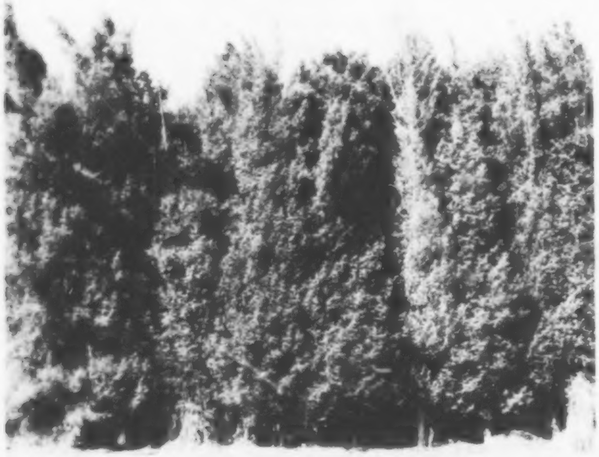

Figure 2—*A pure stand of California-laurel about 90 years old near Roseburg, OR. Tree crowns form a dense exterior border.*

canopy is particularly dense and extensive, understory vegetation may almost be limited to mosses, ferns, and laurel seedlings *(7,51)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—California-laurel flowers regularly and often profusely. The pale yellow, perfect flowers, 15 mm (0.6 in) in diameter, grow on short-stemmed umbels that originate from leaf axils or near the terminal bud. Flower buds develop early; those for the following year become prominent as current-year fruits are maturing. Flowering within the long north-south range of California-laurel has occurred in all months from November to May, beginning before new leaves appear *(24,25,29,61)*. The flowering period may stretch into late spring and summer by the occasional appearance of flowers originating in axils of developing leaves *(48)*. California-laurel flowers at an early age; flowers have been observed on short whiplike shrubs and on 1-year-old sucker growth that originated on a long broken stub *(50)*. Small insects appear to be the chief pollinators *(25)*.

The fruits—acrid drupes each containing a single, thin-shelled, nutlike seed 15 mm (0.6 in) in diameter—ripen in the first autumn after flowering *(52)*. As drupes mature, their thin, fleshy hull changes from medium green to speckled yellow-green, pale yellow, or various other hues from yellow-green tinged with dull red or purple through purplish brown to purple. Ripe drupes may be yellow-green on one tree, dark purple on an adjacent tree *(11)*.

Seed Production and Dissemination—Seed crops are abundant in most years. Although umbels bear four to nine flowers each, generally only one to three fruits set *(24)*. The age when a tree first bears fruit, the age for maximum production, and the average quantity produced have not been determined. Seeds are produced in abundance after trees are 30 to 40 years old *(20)*.

Drupes fall stemless to the ground in late autumn or winter and are dispersed by gravity, wind, animals, and water *(34)*. Fallen drupes are easily gathered by hand. The drupes are large and heavy; 454 g (1 lb) of drupes may yield about 300 cleaned seeds *(39)*.

Under favorable natural conditions, seeds on the ground retain viability over winter, but, under adverse conditions, viability may prove very transient. Viability has been maintained for 6 months when seeds were stored at 3° C (37° F) in wet, fungicide-treated vermiculite *(34)*.

Fresh, untreated seeds germinate indoors or outdoors in peat moss, sawdust, vermiculite, or light-textured soil but may require 3 months or longer *(25,39,60)*. Germination can be speeded by scarifying, cracking, or removing the endocarp, or stratifying the seed, but up to 2 months may still be required *(25,34,60)*. In comparison tests made in petri dishes, California-laurel germination was highest in 30 days under a temperature regime of 16° C (61° F) day, 7° C (45° F) night, and when evaporative stress was minimal *(34)*. Germination did not appear to be affected by light level but was highest in soil with moisture tension at 4 to 10 atmospheres.

Seedling Development—Germination occurs naturally in autumn soon after seedfall, or in late winter and spring *(52)*. Covered seeds germinate best, but the large seeds are not buried readily without ground disturbance or silt deposition by high water. Seedling establishment is not common in the drier parts of California except in protected areas and where ground is disturbed *(24)*. California-laurel seedlings invade grasslands and brushlands in the Berkeley Hills; similar capabilities were observed in the Santa Cruz Mountains *(34,61)*.

Germination is hypogeal, and the fleshy cotyledons remain within the endocarp and attached to the seedling until midsummer, when the plant may be 15 to 20 cm (6 to 8 in) tall *(25,48)*. Generally there

Table 1—Trees, shrubs, and herbs associated with California-laurel in different parts of its range[1]

Trees	Shrubs	Herbs
Abies grandis	*Adenostoma fasiculatum*	*Actaea rubra*
Acer circinatum	*Amelanchier* spp.	*Adiantum pedatum*
Acer macrophyllum	*Arctostaphylos canescens*	*Antennaria suffrutescens*
Acer negundo	*Arctostaphylos columbiana*	*Arnica spathulata*
Aesculus californica	*Arctostaphylos hispidula*	*Aster radulinus*
Alnus rhombifolia	*Arctostaphylos mariposa*	*Balsamorhiza deltoides*
Alnus rubra	*Arctostaphylos nevadensis*	*Blechnum spicant*
Arbutus menziesii	*Arctostaphylos patula*	*Boykinia* spp.
Castanopsis chrysophylla	*Arctostaphylos tomentosa*	*Cheilanthes siliquosa*
Ceanothus thyrsiflorus	*Arctostaphylos viscida*	*Chimaphila umbellata*
Cercis occidentalis	*Artemisia californica*	*Chlorogalum pomeridianum*
Chamaecyparis lawsoniana	*Baccharis pilularis*	*Convolvulus polymorphus*
Cornus nuttallii	*Berberis* spp.	*Diplacus aurantiacus*
Corylus cornuta	*Ceanothus* spp.	*Disporum* spp.
Eucalyptus globulus	*Cornus californica*	*Dryopteris arguta*
Fraxinus dipetala	*Eriodictyon californicum*	*Eriophyllum lanatum*
Fraxinus latifolia	*Garrya buxifolia*	*Erythronium oregonum*
Garrya elliptica	*Garrya fremontii*	*Fragaria californica*
Heteromeles arbutifolia	*Gaultheria shallon*	*Galium* spp.
Libocedrus decurrens	*Holodiscus discolor*	*Hieracium cynoglossoides*
Lithocarpus densiflorus	*Juniperus communis*	*Hierochloe occidentalis*
Myrica californica	*Juniperus sibirica*	*Horkelia sericata*
Picea sitchensis	*Lonicera hispidula*	*Iris* spp.
Pinus attenuata	*Lotus scoparius*	*Juncus* spp.
Pinus contorta	*Lupinus albifrons*	*Linnaea borealis*
Pinus coulteri	*Myrica hartwegii*	*Lomatium* spp.
Pinus jeffreyi	*Pickeringia montana*	*Lupinus nanus*
Pinus lambertiana	*Quercus dumosa*	*Marah fabaceus*
Pinus monticola	*Quercus durata*	*Mimulus guttatus*
Pinus ponderosa	*Quercus sadleriana*	*Osmorhiza chilensis*
Pinus sabiniana	*Quercus vaccinifolia*	*Oxalis oregana*
Platanus racemosa	*Rhamnus californica*	*Pellaea mucronata*
Populus trichocarpa	*Rhamnus crocea*	*Pityrogramma triangularis*
Prunus ilicifolia	*Rhododendron californicum*	*Polypodium vulgare*
Pseudotsuga menziesii	*Rhododendron macrophyllum*	*Polystichum munitum*
Quercus agrifolia	*Rhododendron occidentale*	*Pteridium aquilinum*
Quercus chrysolepis	*Rhus diversiloba*	*Pyrola dentata*
Quercus douglasii	*Ribes* spp.	*Sanicula crassicaulis*
Quercus garryana	*Rosa gymnocarpa*	*Satureja douglasii*
Quercus kelloggii	*Rubus laciniatus*	*Scrophularia californica*
Quercus lobata	*Rubus parviflorus*	*Selaginella bigelovii*
Quercus wislizeni	*Rubus procerus*	*Senecio bolanderi*
Robinia pseudoacacia	*Rubus spectabilis*	*Smilacina stellata*
Salix spp.	*Rubus ursinus*	*Stachys rigida*
Sambucus spp.	*Rubus vitifolius*	*Synthyris reniformis*
Sequoia sempervirens	*Symphoricarpos albus*	*Trientalis latifolia*
Taxus brevifolia	*Symphoricarpos mollis*	*Trillium ovatum*
Thuja plicata	*Symphoricarpos rivularis*	*Vicia* spp.
Torreya californica	*Vaccinium* spp.	*Viola* spp.
Tsuga heterophylla	*Whipplea modesta*	*Xerophyllum tenax*

[1] Sources: *2,7,10,14,15,22,32,35,38,47,51,55,61,63*

are two large cotyledons, sometimes three, and no endosperm. Seedlings produce leaves of several transitional forms as they develop and do not branch until they are 2 or 3 years old unless induced tc do so by removal of the terminal bud. They soon develop a moderately stout taproot and are difficult to transplant if more than 1 year old unless grown in containers. Recovery after transplanting is often slow, and height growth may be limited for several seasons.

Young California-laurel seedlings appear flexible in their growth requirements. In the first 120 days, seedlings potted in vermiculite grew well at several levels of temperature, evaporative stress, soil moisture, and soil nutrients *(34)*. Seedlings grown at 18 percent or more of full sunlight produced the most dry weight.

Vegetative Reproduction—California-laurel can be reproduced by cuttings *(60)*, but techniques need further development. Under natural conditions, it may sprout prolifically from the root collar, stump, and trunk. Sprouts and suckers develop wherever a canopy opening admits strong light from the side or overhead. Stumps ringed with root-collar sprouts and both fallen and standing live trunks entirely enveloped in new green sucker growth are common *(24)*. Crowns formed by clumps of sprouts growing in the open typically assume a distinctive, very dense, and symmetrically rounded shape *(12,50)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Over much of its range, California-laurel attains heights of 12 to 24 m (40 to 80 ft) and diameters of 46 to 76 cm (18 to 30 in). On protected bottom lands of southwestern Oregon and northern California, mature trees are 91 to 183 cm (36 to 72 in) in d.b.h. and 30 m (100 ft) or more in height *(20,24)*. A maximum d.b.h. of 404 cm (159 in) *(1)* and a maximum height of 53.3 m (175 ft) have been reported *(49)*.

California-laurel occurs as a noncontiguous forest type on about 76 080 ha (188,000 acres), 9 712 ha (24,000 acres) in Oregon and 66 368 ha (164,000 acres) in California *(4,17)*. As a component of conifer or other hardwood types, it occurs on an additional 437 060 ha (1,080,000 acres) in California and an undetermined additional acreage in Oregon. Total growing stock volume is approximately 14.7 million m^3 (520 million ft^3). In California, the mean stand growing-stock volume in the type is 117 m^3 per ha (1,677 ft^3/acre), with a maximum of about 218 m^3 per ha (3,125 ft^3/acre).

The growth rate of California-laurel varies greatly because of the many climatic, soil, and competitive conditions in which it occurs. Several observers report its height growth is slow, about 0.3 m (1 ft) per year, but on good sites in southern Oregon, height growth averages between 0.3 and 0.6 m (1 to 2 ft) per year *(3,12,51)*. Growth of trees from seed to 38 or 41 cm (15 or 16 in) diameter in 50 years has been reported *(57)*. Total number of stems 10 cm (4 in) in d.b.h. or larger in California and Oregon stands with a large component of California-laurel ranged from 245 to 2,402/ha (99 to 972/acre) (fig. 3); reported basal areas ranged from 34.0 to 167.4 m^2/ha (148 to 729 ft^2/acre) *(51,61,62)*.

Multiple trunks frequently develop in both open-grown and closed stands of California-laurel. Trees in the open often attain a crown spread greater than their height and may not develop a well-defined upper trunk. Many forest-grown trees also fork repeatedly; forking within 3 m (10 ft) of the ground is common (fig. 3). Generally each fork grows vertically and side branches die. Adjacent forked and unforked trees make similar height growth.

Rooting Habit—The root system of California-laurel has been described as fleshy, deep, and widespreading *(49)*. Several exceptions have been noted, however. Root wads of windthrown trees from alluvial soil in southern Oregon were limited in extent and without a prominent taproot *(50)*. Root systems of seedlings and young trees dug near Berkeley, CA, had relatively shallow root systems, as did some fallen older trees *(28)*. Over half the roots in representative California-laurel stands in the Berkeley Hills were distributed in the top 30 cm (12 in) of Los Osos adobe clay and all were in the top 90 cm (36 in) *(34)*. In contrast to the paucity of information on the shape and extent of the root system of California-laurel, its root structure has been thoroughly investigated *(26,27)*.

Reaction to Competition—California-laurel is generally classed as shade tolerant, but the tolerance level is not well defined. A very dense canopy is formed by its thick evergreen leaves, which persist 2 to 6 years. The presence of many small seedlings but no saplings under some closed canopies and the development of long boles clear of live limbs indicate that laurel is not always tolerant of its own shade (fig. 4). These indicators are no criteria of tolerance relative to other species, however, and laurel trees are common among moderately dense conifers.

In some localities, California-laurel appears to be the climax vegetation *(7,24,34,61)*. It is relatively long lived, reproduces from both seeds and sprouts,

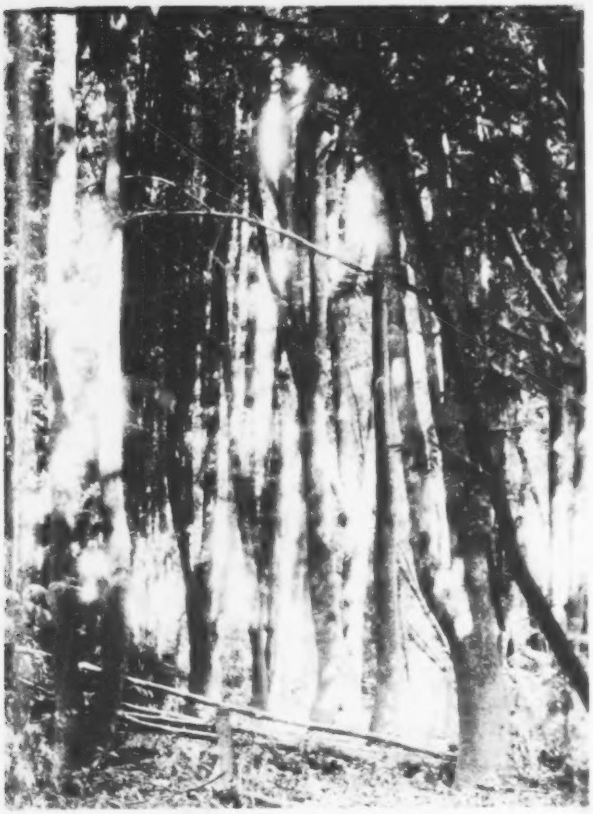

Figure 3—*One vigorous, 90-year-old stand of pure California-laurel averaged 712 stems per hectare (288/acre) 18 cm (7 in) in d.b.h. or larger.*

forms dense pure canopies, and appears to have few serious natural enemies. California-laurel reproduces itself at natural light intensities of 1 to 5 percent of full sunlight; the most dry weight in one experiment was produced at 18 percent of full sunlight, but growth was also reasonable at 8 percent *(34,61)*.

Allelopathic influences have been suspected as the cause of more bare ground under canopy of California-laurel than under canopy of associated trees. Bioassay experiments showed that the leaf and litter volatiles, leachates, and extracts of laurel are capable of inhibiting germination and growth of several test species *(56,61)*.

The distribution of California-laurel in the Coast Ranges south of San Francisco appears to represent a vegetational continuum *(61)*. About the same mixture of understory plants was found under California-laurel canopies as under associated trees, but California-laurel and some of its associates seemed to have a greater tendency to spread to other communities than species from those communities to invade California-laurel woodland.

Damaging Agents—Wind and snow cause appreciable destruction and deformation in California-laurel stands. Blowdown is common during severe wind and rain storms in California and Oregon *(24,51)*. Wet clinging snow abets windthrow, breaks tops, and splits forks. Striking examples of crown deformation and molding by strong winds are numerous near the coast.

Because of its thin bark, the tree is easily top-killed by fire, but it sprouts rapidly. Dense clumps

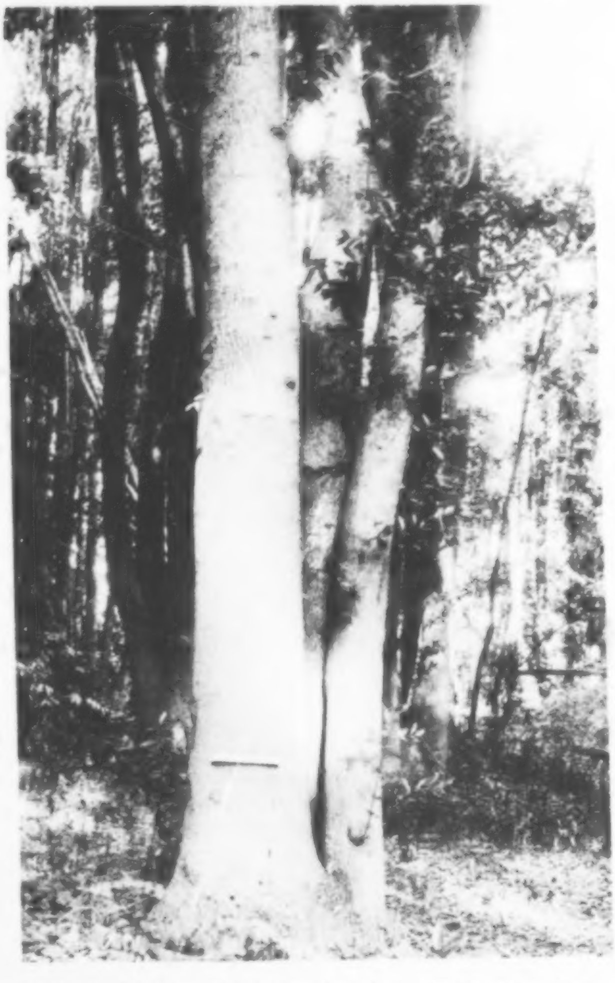

Figure 4—*Branches of California-laurel are shaded out in dense stands, but new shoots readily develop when the trunk is again exposed to sufficient light.*

are often formed on cutover land, which may prevent the establishment of desired conifers. Very young California-laurel seedlings have less capacity than dwarf chaparral broom (*Baccharis pilularis*) or coast live oak (*Quercus agrifolia*) to resprout after complete destruction by heat at ground level *(34)*.

California-laurel is relatively tolerant to boron. In comparison tests, it was less tolerant to boron than Digger pine (*Pinus sabiniana*) but more tolerant than Pacific madrone (*Arbutus menziesii*) or bigleaf maple (*Acer macrophyllum*) *(18)*.

More than 40 species of fungi have been observed on California-laurel, and perhaps three (*Anthostoma oreodaphnes*, *Nectria umbellulariae*, and *Sphaerella umbellulariae*) are restricted to this species *(48)*. Few fungi cause serious damage to the living tree. In central coastal California, a severe outbreak of laurel leaf blight followed abnormally heavy precipitation in two of three winters. A bacterium, *Pseudomonas lauracearum*, and two fungi, *Kabatiella phoradendri* f. sp. *umbellulariae* and *Colletotrichum gloeosporioides*, were isolated from affected leaves *(42)*. No trees were killed and crowns leafed out anew the following year. Dieback of twigs and new shoots was substantial, however, and was followed by scattered dieback of branches up to 2.5 cm (1 in) in diameter associated with a *Botryosphaeria* sp., a fungus that has been blamed for much damage to this species *(23)*. Incidence of infection by endophytic fungi, primarily *Septogloeum* sp., averaged 25 percent for leaf samples of California-laurel collected from four sites representing an environmental gradient in southwestern Oregon *(44)*. Several sooty molds and other diseases are found on laurel leaves; the stem canker, *Nectria galligena*, occurs primarily where snow, ice, or wind cause severe bending and cracks in the bark of stems and branches; and *Ganoderma applanatum* fruits readily on scarred trees.

Wood rot is common in California-laurel. Various fungi cause decay associated with wounds, and *G. applanatum* may function as a heart rot in live wood *(23)*. Even in young stands, dead knots, stem malformations, and root collars are often decayed. Cull in one northern California study averaged 7 and 10 percent of the gross cubic volume in trees of saw log or cordwood size and quality, respectively *(31)*.

California-laurel has no serious insect enemies. A leafblotch miner (*Lithocolletis umbellulariae*), a stag beetle (*Dichelonyx valida*), and a thrips (*Thrips madronii*) cause some damage to leaves. The cottonycushion scale (*Icerya purchasi*) used to be very damaging but is now under control *(48)*. Several wood borers and beetles attack dead parts of the tree; but only the powderpost beetle (*Ptilinus basalis*) that attacks dead and stored wood and oak bark beetles (*Pseudopityophthorus* spp.) that infest injured, felled, and recently dead trees cause damage of economic consequence *(16)*.

Except for seed consumption, animal damage to California-laurel appears minor. In some localities and situations, browsing damage to seedlings and new sprout growth may be of consequence. Young laurel seedlings are browsed less than some associated species *(34)*.

Special Uses

Wood of California-laurel compares favorably in machining quality with the best eastern hardwoods *(8)* and is used for fancy turned woodenware, interior trim, cabinets, furniture, paneling, veneer, and gunstocks. Burls and other growths with unusual grain are especially prized for making gifts, novelties, and wood carvings, all marketed as myrtlewood. The wood of mature trees is moderately heavy, hard, fine grained, rich yellowish brown to light gray, and often beautifully mottled. The wood of younger trees generally has less distinctive grain and markings. By rough estimate, 19 950 to 22 800 m^3 (3.5 to 4 million fbm) are used annually in the myrtlewood industry.

Indians and early settlers used all parts of the tree for food and medicinal purposes *(6,21)*. Leaves are still collected and dried for home use and commercial sale as a food seasoning *(5,37,61)*. The leaves, seeds, and wood have strong chemical properties and should be used for food, seasoning, or medicinal purposes with caution *(5,9,36,48,61)*.

California-laurel is used for hedges, windbreaks, and indoor and outdoor ornamental evergreens *(3,29,41,43)*. It also provides food and cover for wildlife *(53)*. Silver gray squirrels, dusky-footed woodrats, California mice, and Steller's jays feed extensively on the seeds *(54,55)*. Hogs eat both seeds and roots. Young sprouts are choice browse for deer and goats in spring and summer *(33,47)* when volatile components of leaves are at lowest concentrations *(30)*.

Genetics

Several racial variations are recognized. *Umbellularia californica* forma *pendula* Rehd. is an uncommon, broad-spreading tree distinctive for its pendulous branchlets that contrast strongly with typically ascending branch growth *(24,45)*. *Umbellularia californica* var. *fresnensis* Eastwood has fine white down on the lower surfaces of leaves and on branches of the panicle *(11)*. Gregarious, rockpile, dwarf, and prostrate forms *(24)* may indicate other varietal differences.

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Glossary

Russell M. Burns and Barbara H. Honkala

Acicular foliage—Needle-shaped leaves.

Acropetal—Developing upward from the base toward the apex.

Adventitious—Plant organs produced in an unusual or irregular position, or at an unusual time of development.

Aerobic—Capable of living only in the presence of free oxygen.

Afterripening—Enzymatic process occurring in seeds, bulbs, tubers, and fruit after harvesting; often necessary for germination or resumption of growth.

Air layering—Inducing root development on an undetached aerial portion of a plant, commonly by wounding it, treating it with a rooting-stimulant, and wrapping it in moist material under a waterproof covering, so that the portion so treated is capable of independent growth after separation from the mother plant.

All-aged—A condition of a forest or stand that contains trees of all or almost all age classes. It is generally a primary stand where individuals have entered at various times when and where space permitted. (*See* **Uneven-aged**).

Allele—One of an array of genes possible at a certain position (locus) on a given chromosome.

Allelopathy—The influence of plants, other than microorganisms, upon each other, arising from the products of their metabolism.

Allopatric—Occurring in different areas or in isolation. (*Cf.* **Sympatric**).

Alluvial--A type of azonal soil which is highly variable and is classified by texture from fine clay and silt soils through gravel and boulder deposits.

Alluvium—Soil, usually rich in minerals, deposited by water, as in a floodplain.

Alpha pinene—A hydrocarbon of the terpene class occurring in many essential oils; it has a density of about 0.855 and an index of refraction of about 1.465, both at 25° C (77° F).

Anaerobic—Capable of living in the absence of, or not requiring, molecular oxygen.

Andesite—An extrusive usually dark grayish rock consisting essentially of oligoclase or feldspar.

Anemophilous--Normally wind-pollinated.

Anther—The part of the stamen that develops and contains pollen.

Anthesis—The time at which a flower comes into full bloom.

Apophysis—The rounded, exposed thickening on the scales of certain pine cones.

Appalachian Highlands—The lands of the Appalachian Mountains extending from central New York south to northeastern Alabama.

Arbuscula—A small or low shrub having the form of a tree.

Argillite—A compact argillaceous (clayey) rock differing from shale in being cemented by silica and from slate in having no slaty cleavage.

Arillate—Having an aril (an appendage, outgrowth, or outer covering of a seed, growing out from the hilum or funiculus).

Auxin—A natural hormone that regulates plant growth, generally identified with β-indolylacetic acid (IAA), a heteroauxin.

Backcross—A cross between a hybrid and either one of its parents.

Basalt—A dark gray to black colored, dense to fine-grained igneous rock.

Basipetal—Developing toward the base from the apex.

Batture—Land between the river and the manmade levees that border it.

Berry—A simple, pulpy fruit of a few or many seeds (but no stones) developed from a single ovary.

Beta phellandrene—A terpene with a density of about 0.84 and an index of refraction of about 1.48, both at 25° C (77° F).

Beta pinene—A terpene with a density of about 0.867 and an index of refraction of about 1.477, both at 25° C (77° F).

Biomass--The total quantity, at a given time, of living organisms of one or more species usually expressed in weight per unit area.

Bisexual—Having both male and female sexual reproductive structures.

Bonsai—The culture of miniature potted trees, which are dwarfed by stem and root pruning and controlled nutrition.

Boreal forest—A coniferous forest of the northern hemisphere characterized by evergreen conifers such as spruce, fir, and pine.

Breast height—1.37 m or 4.5 ft above groundline on standing trees, a standard height in USA for recording diameter, girth, or basal area.

Campanulate—Bell-shaped.

Canadian Shield—The Precambrian nuclear mass centered in Hudson Bay around which, and to some extent upon which, the younger sedimentary rocks have been deposited.

Canopy—The more or less continuous cover of branches and foliage formed collectively by the crowns of adjacent trees.

Capsule—A dry usually many-seeded fruit composed of two or more fused carpels that split at maturity to release their seeds.

Carr—A deciduous woodland on a permanently wet, organic soil.

Catena—A sequence of different soils, generally derived from similar parent soil material, each of which owes its character to its peculiar physiographic position.

Catkin—A drooping elongated cluster of bracted unisexual flowers found only in woody plants.

Chromosome—A microscopic, usually rod-like body carrying the genes. Number, size, and form of chromosomes are usually constant for each species.

Cirque—A deep, steep-walled basin shaped like a half bowl, on a mountain.

Clearcut—The cutting method that describes the silvicultural system in which the old crop is cleared over a considerable area at one time. Regeneration then occurs from (a) natural seeding from adjacent stands, (b) seed contained in the slash or logging debris, (c) advance growth, or (d) planting or direct seeding. An even-aged forest usually results.

Cleft graft—The stock is cut off, split, and then one or more scions are placed in this cleft (split) making the cambium layers of the stock and scion match.

Climax community—The terminal stage of an ecological succession sequence which remains relatively unchanged as long as climatic and physiographic factors remain stable.

Clinal—Sloping.

Clone—Any plant propagated vegetatively and therefore considered a genetic duplicate of its parent.

Codominant (a crown class)—Species in a mixed crop that are about equally numerous and vigorous forming part of the upper canopy of a forest, less free to grow than dominants but freer than intermediate and suppressed trees.

Collenchyma—Flexible, supportive plant tissue usually of elongated living cells with unevenly thickened walls which are usually interpreted as primary walls.

Colluvium—Rock detritrus and soil accumulated at the foot of a slope.

Conglomerate—Made up of parts from various sources or of various kinds.

Corymb—A flat-topped floral cluster with outer flowers opening first.

Cotyledon—An embryonic leaf, which often stores food materials, characteristic of seed plants.

Crown class—Any class into which trees of a stand may be divided based on both their crown development and crown position relative to crowns of adjacent trees. The four classes commonly recognized are dominant, codominant, intermediate, and suppressed.

Culmination of mean annual increment—For a tree or stand of trees, the age at which the average annual increment is greatest. It coincides precisely with the age at which the current annual increment equals the mean annual increment of the stand and thereby defines the rotation of a fully stocked stand that yields the maximum volume growth.

Cultivar—A contraction of "cultivated variety." It refers to a plant type within a particular cultivated species that is distinguished by 1 or more characters.

Current annual increment (CAI)—The amount by which the volume of a tree or stand increases in 1 year.

Cymose—Bearing a cyme, a more or less flat-topped floral cluster with the central flowers opening first.

Cytokinins—A class of hormones that promote and control growth responses of plants.

Dehisce—To split open when ripe, usually along definite lines or sutures to release seeds.

Deliquescent branching—A mode of branching in trees in which the trunk divides into many branches leaving no central axis, as in elms. (*See* **Excurrent branching.**)

Destructive distillation—The decomposition of wood by heating out of contact with air, producing primarily charcoal.

Diallel cross—Complete: a mating design and subsequent progeny test resulting from the crossing of *n* parents in all possible n^2 combinations including selfs and reciprocals. Incomplete: a partial sampling—any individual family or type of family may be omitted. In either type of cross, identities of both seed and pollen parents are maintained for each family.

Dichogamy—In a perfect flower, maturation of stamens and pistils occurs at different times, thus preventing self-pollination.

Dioecious—Having staminate (male) flowers and pistillate (female) flowers on different plants of the same species.

Diorite—A granular crystalline igneous rock commonly of acid plagioclase and hornblende, pyroxene, or biotite.

Diploid—An organism which has two sets of chromosomes in its cells, paternal and maternal.

Disclimax—A relatively stable ecological community often including kinds of organisms foreign to the region and replacing the climax because of disturbance.

DNA—Deoxyribonucleic acid, the carrier of genetic information (genes) in cells.

Dominant (a crown class)—One of four main crown classes recognized, on a basis of relative status and condition in the crop. Dominant trees have their crowns in the uppermost layers of the canopy and are largely free-growing.

Duff—The partially decomposed organic matter (litter of leaves, flowers, and fruits) found beneath plants, as on a forest floor.

Ecotone—Any zone of intergradation or interfingering, narrow or broad, between contiguous plant communities.

Ecotype—A subgroup within a species, which is genetically adapted to a habitat type that is different from the habitat type of other subgroups of that species. It normally has a large geographical distribution.

Ectotrophic mycorrhiza (ectomycorrhiza)—A mycorrhiza growing in a close web on the surface of an associated root; generally formed by basidiomycete fungi.

Edaphic—Pertaining to the soil in its ecological relationships.

Endocarp—The innermost differentiated layer of the pericarp, or fruit wall, as in the stoney part of a drupe.

Endosperm—A nutritive tissue in seed plants formed within the embryo sac.

Endotrophic mycorrhiza (endomycorrhiza)—A mycorrhiza penetrating into the associated root and ramifying between the cells; generally formed by phycomycete fungi.

Epicotyl—The portion of the axis of an embryo or young seedling above the point where the cotyledon(s) is attached.

Epigeal—The part of the seedling above the cotyledon(s). (*Cf.* **Hypogeal).**

Epiphyte—An organism that grows on another plant but is not parasitic on it.

Even-aged management—The application of a combination of actions that results in the creation of stands in which trees of essentially the same age grow together. The difference in age between trees forming the main canopy level of a stand usually does not exceed 20 percent of the age of the level of a stand at maturity. Regeneration in a particular stand is obtained during a short period at or near the time that a stand has reached the desired age or size for regeneration, and is harvested. Cutting methods producing even-aged stands are clearcut, shelterwood, or seed tree.

Exalbuminous—Descriptive of seeds that lack endosperm.

Excurrent branching—Tree growth in which the main axis continues to the top of the tree from which smaller, lateral branches arise (as in conifers). (*See* **Deliquescent branching.**)

Fastigiate form—Strictly erect and more or less parallel vertical branches.

Fbm—Foot (feet) board measure (board foot [feet]).

Fen—A bog with springs as a water source other than precipitation.

Feral goats—Goats that have escaped from domestication and become wild.

Fluvial—Produced by stream action.

Frost rings—A zone of injured cambium tissue caused by frost.

Funiculus—The basal stalk of an ovule arising from the placenta in the angiosperms.

Gabbro—A dark, coarse-textured, heavy rock composed of calcium feldspar and augite with a small amount of quartz.

Gene—The smallest transmittable unit of genetic material consistently associated with a single primary genetic effect.

Genet—A single sexually produced individual.

Germinative capacity—Percentage of seeds that germinate during the normal period of germination.

Germplasm—Within an individual or group the collective materials that are the physical basis for inheritance.

Gibberellin—A plant hormone useful in regulating the growth characteristics of many plants.

Glade—An open space in a forest.

Gneiss—A metamorphic rock derived from either igneous or sedimentary formations.

Graft incompatibility—Said of plants which, when grafted together, fail to form a lasting union.

Granite—A very hard natural igneous rock formation.

Grood soils—Nut-structured soils characteristic of the transition zone between prairie soils and podzolic soils, i.e., prairie-forest soils.

Group selection—The cutting method which describes the silvicultural system in which trees are removed periodically in small groups resulting in openings that do not exceed 0.4 to 0.8 hectare (1 to 2 acres) in size. This leads to the formation of an uneven-aged stand in the form of a mosaic of age-class groups in the same forest.

Growing stock level (GSL)—A numerical index. The residual square meters of basal area per hectare (square feet of basal area per acre) when the average stand diameter is 25 cm (10 in) or more in d.b.h. Basal area retained in a stand with an average d.b.h. of less than 25 cm (10 in) is less than the designated level.

Haploid—An organism with one basic chromosome set symbolized by *n*.

Harden-off—The process of gradually reducing the amount of water and lowering the temperature for plants in order to toughen their tissues, making it possible for them to withstand unfavorable (usually cold) environmental conditions.

Hedging—Close-cropping.

Heptane—Any of several isometric hydrocarbons of the methane series.

Hermaphrodite (bisexual)—A flower with both functional male and female reproductive organs.

Heterozygote—An organism whose cells have one or more sets of unlike alleles.

High-lining—The underside of a forest canopy that is uniformly cropped by deer at the highest level they can browse. A browseline.

Hilum—The scar on a seed marking the point of attachment of the ovule.

Hybrid swarm—An extremely variable population derived from the hybridization of two different taxa and consisting of the products of subsequent segregation and recombination, backcrossing, and crossing between the hybrids themselves. It occurs where the range of inter-fertile species overlap.

Hydroponics—The cultivation of plants, without soil, in water solutions of nutrients required for growth.

Hydrosere—An ecological sere (plant community) originating in an aquatic habitat.

Hypanthium—A floral tube formed by the fusion of the basal portions of the sepals, petals, and stamens and from which the rest of the floral parts emanate.

Hypocotyl—The part of an embryo or seedling below the cotyledon(s) and above the radicle (but sometimes including it).

Hypogeal—Describes seed germination in which the colytedons remain beneath the surface of the soil. *(Cf.* **Epigeal).**

Hypogeous—Growing or developing below the soil surface.

Igneous rock—Formed by solidification of molten magma.

Imperfect flower—A flower which lacks either stamens or carpels.

Inbreeding—In plants, a breeding system in which sexual reproduction involves the interbreeding of closely related plants by self-pollination or backcrossing.

Individual tree selection—The cutting method that describes the silvicultural system in which trees are removed individually, here and there, each year over an entire forest or stand. The resultant stand usually regenerates naturally and becomes all-aged.

Indolebutyric acid (IBA)—A synthetic auxin widely used in horticulture to induce rooting of cuttings.

Inland Empire—A region in eastern Washington, northern Idaho, and western Montana, named for commercial purposes.

Intergeneric—Existing or occurring between genera.

Intermediate (a crown class)—A tree of the middle canopy dominated by others in the dominant and codominant crown classes.

Intermountain—In the Forest Service, an area that includes the States of Montana, Idaho, Utah, Nevada, and the western quarter of Wyoming.

Intraspecific—Refers to some relationship between the members of the same population or species.

Introgression—The entry or introduction of a gene from one gene complex to another.

Isoline—Isogram; a line on a map or chart along which there is constant value (temperature, pressure, or rainfall).

Isozymes (isoenzymes)—Any two or more chemically distinct but functionally like enzymes.

Jackstrawed fuel—Trees that have fallen in tangled heaps.

Juvenile cuttings—The youngest parts of the branches are severed from the plant and rooted to produce new plants.

Karyotype—The character of the chromosomes as defined by their size, shape, and number.

Knee—An abrupt bend in a stem or tree trunk, or an outgrowth rising from the roots of some swamp-growing trees such as baldcypress.

Krummholz—The stunted growth habit, literally crooked wood, caused by wind and found in certain tree species at their upper limit of distribution.

Cushion krummholz—Alpine trees exposed to severe wind conditions are wind-pruned to a cushion-like mat.

Flagged krummholz—The tallest trees protrude from the protective snow pack and become wind-battered "flags."

Lacustrine—Related to or growing in lakes.

Lake Agassiz Basin—A late glacial and early post-glacial lake area in southern North Dakota and western Minnesota.

Lake States—Those States bordering the Great Lakes, that is, Minnesota, Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York.

Lammas—The part of an annual shoot that is formed after a summer pause in growth.

Layering—The rooting of an undetached branch, laying on or partially buried in the soil, which is capable of independent growth after separation from the mother plant.

Leaf area index (LAI)—Leaf surface area per unit of land surface area. For broad-leaf forests, the index is calculated using only one side of the leaf blade; for needle-leaf stands the total leaf surface is used; and, for mixed broad- and needle-leafed stands, a combination of the two is used.

Lightwood (fatwood, lightered wood or stumps, stumpwood)—Coniferous wood having an abnormally high content of resin and therefore easily set alight (afire).

Lignotubers—A woody swelling at ground level originating from the axils of the cotyledons from whose concealed dormant buds a new tree can develop if the old one is injured. Characteristic of many Eucalypts.

Limonene—A component of pine turpentine with a density of approximately 0.84 and an index of refraction of about 1.47, both at 25° C (77° F).

Litter—The uppermost layer of organic debris on a forest floor consisting essentially of freshly fallen or only slightly decomposed vegetable matter, mainly foliage but also bark, twigs, flowers, and fruits. The L-layer of the organic portion of the soil profile.

Loess—A uniform and unstratified fine sand or silt (rarely clay) deposit transported by wind (an aeolian soil). It is sometimes described as rock flour.

Lumen—Either the cell cavity or a unit of luminous flux equal to the light emitted by a uniform point source of one candle intensity.

Lye—A strong alkaline solution of sodium hydroxide, potassium hydroxide, or the leachate of wood ashes that is rich in potassium carbonate.

Maceration—The process of removing the fleshy tissue surrounding seeds, often by soaking in water.

Macronutrients—The nutritional elements, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur, essential for normal plant growth, development, and reproduction. They are usually derived from the soil.

Mean annual increment (M.A.I. or m.a.i.)—The total increment of trees in a stand up to a given age, divided by that age, usually expressed in annual cubic meters of growth per hectare (cubic feet of growth per acre).

Megagametophyte—The female gametophyte which develops from the megaspore and produces the female gamete(s).

Megasporangium—The sporangium in which megapores are produced; the nucellus of seed plants.

Megaspore—In plants having two types of haploid spores (microspores (male) and megaspores (female)), megaspores give rise to megagametophytes.

Meiosis—Reduction division resulting in the production of haploid gametes; a process consisting of two specialized nuclear divisions ultimately leading to the formation of eggs or sperm.

Meristem—Tissue primarily associated with protoplasmic synthesis and formation of new cells by division.

Mesic—Characterized by intermediate moisture conditions, neither decidedly wet nor decidedly dry.

Mesophyte—A plant whose normal habitat is neither very wet nor very dry.

Mesozoic—An era of geologic history marked by the cycads, evergreen trees, dinosaurs, marine and flying reptiles, and ganoid fishes.

Metamorphism—A pronounced change effected by pressure, heat, and water that results in a more compact and more highly crystalline condition.

Micronutrients (trace elements)—Nutritional elements necessary in minute quantities for normal plant growth, such as boron and manganese.

Micropyle—A minute opening in the integument of an ovule through which the pollen tube normally passes to reach the embryo sac, usually closed in the mature seed to form a superficial scar.

Microsporangium—In plants having two types of haploid spores (microspores and megaspores), the saclike structure in which microspores are produced.

Microspore—A haploid spore produced by meiosis of the microsporocyte and developing into the male gametophyte. The pollen grain of seed plants.

Mine spoil—Earth and rock excavated from a mine.

Mitosis—Normal division of a nucleus into two identical daughter nuclei by a process of duplication and separation of chromosomes.

Monadnock—A hill or mountain of resistant rock surmounting land of considerable area and slight relief shaped by erosion.

Monoecious—Having staminate and pistillate flowers in separate places on the same plant.

Montane—The biogeographic zone made up of relatively moist cool upland slopes below timberline that is characterized by large evergreen trees as a dominant life form.

Mor—A layer of organic material made up of largely unrecognizable plant debris and their decomposition products overlain by litter and lying on the surface of, and essentially unmixed with, the mineral soil. Earthworms are absent.

Muck—Highly decomposed organic material formed under conditions of waterlogging, with few recognizable remains of the original plants.

Mull—A soil whose upper mineral layer has become intimately mixed (mainly through the action of earthworms) with amorphous organic material, sometimes to a depth of 1.2 to 1.5 meters (4 to 5 feet).

Mycelium—The mass of threadlike filaments constituting the vegetative body of a fungus.

Natural pruning (self pruning)—The freeing of the stem of a standing tree of its branches by natural death, disintegration, and/or fall, from such causes as decay, or deficiency of light or water, or snow, ice, and wind breakage.

Naval stores—The products of the resin industry. In the United States they are turpentine, rosin, pine tars, and pitch. Gum naval stores refer specifically to gum turpentine and gum rosin; wood naval stores to wood turpentine and wood rosin.

Normal yield table—A table showing, for one or more species in a fully stocked stand, the growth pattern of a managed even-aged stand derived from measurements at regular intervals covering its useful life. It includes mean d.b.h. and height, number of stems, and standing volume per unit area. The table may also contain a variety of other useful data.

North Central—In the Forest Service, an area that includes Indiana, Illinois, Michigan, Wisconsin, Minnesota, Iowa, and Missouri.

Northeastern—In the Forest Service, an area that includes the New England States plus New York, New Jersey, Delaware, Maryland, Pennsylvania, Ohio, West Virginia, and Kentucky.

Nucellus—The tissue of an ovule, in which the female gametophyte (embryo sac) develops; the megasporangium.

Old growth—Stands of forest trees of either seral or climax species growing singly or in association with other tree species. The stands are usually well past the age of maturity as defined by the culmination of mean annual increment and often exhibit characteristics of decadence. These characteristics may include, but are not limited to: low growth rates, dead and dying trees, snags, and down woody material. The stands are usually characterized by large diameter trees relative to species and site potential, multi-layered canopies, a range in tree diameter sizes, and the presence of understory vegetation. The specific attributes of an old-growth stand are primarily dependent on plant associations and forest cover type.

Oleoresin—The nonaqueous secretion of resin acids dissolved in a terpene hydrocarbon oil which is produced in, or exuded from, the intercellular resin ducts of a living tree or accumulated, together with oxidation products, in the dead wood of weathered limbs or stumps. Commonly called pine gum, gum, pitch, or even sap.

Open-grown—In reference to trees, grown in the absence of woody competition.

Operculum—A caplike structure composed of fused sepals and petals that suggests a lid.

Organic soils layers

L-layer—Freshly fallen or only slightly decomposed leaves, twigs, flowers, fruit, and bark lying on the soil surface.

F-layer—Zone of active organic matter fermentation.

H-layer—Humidified zone. The more or less stable fraction from the decomposed soil organic material. Generally, it is amorphous, colloidal, and dark colored.

Ortet—An original plant from which a vegetatively propagated clone has been derived.

Overstory—That portion of the trees in a forest of more than one story forming the upper or uppermost canopy layer.

Ovulate—Bearing or possessing ovules.

Pacific Northwest—In the Forest Service, an area that includes the States of Washington and Oregon.

Pacific Southwest—In the Forest Service, the States of California, and Hawaii plus Guam and the Trust Territories of the Pacific Islands.

Parthenocarpy—The development of fruit without viable seed. It may be induced artificially, as by some foreign pollen, or with hormones.

Peat—Undecomposed or only slightly decomposed organic matter accumulated under conditions of excess moisture. Plant residues show little, if any, morphological change.

Peduncle—A stalk bearing a flower, flower cluster, or a fructification.

Perfect flower—A flower having both stamens and carpels; may or may not have a perianth.

Perianth—A collective term for the floral envelopes, usually the combined calyx and corolla, or tepals of a flower.

Pericarp—The wall of a ripened ovary (fruit) that is homogeneous in some genera and in others is composed of three distinct layers, exocarp, mesocarp, and endocarp.

Permafrost—Permanently frozen ground; generally refers to a layer at some depth below the soil surface. Any layer above it, which thaws in summer, is termed the active layer.

Phenotype—The plant as observed; the product of the interaction of the genes of an organism (genotype) with the environment.

Photoperiodism—The physiological response of an organism to the periodicity and duration of light and darkness which affects many processes including growth, flowering, and germination.

Phyllodes—A flat expanded petiole that replaces the blade of a foliage leaf and which functions in photosynthesis.

Pioneer—A plant capable of invading a newly exposed soil surface and persisting there until supplanted by successor species.

Pistil—Ovule-bearing organ of an angiosperm composed of ovary, style, and stigma. Collectively the pistils are called the genoecium.

Pistillate—Having only female organs. May apply to individual flowers or inflorescences, or to plants of a dioecious species in angiosperms.

Ploidy—Degree of repetition of the basic number of chromosomes.

Plus-tree—A phenotype judged, but not proven by test, to be unusually superior in some quality or qualities.

Podzol—A soil characterized by a superficial layer of raw humus above a generally grey A horizon of mineral soil depleted of sesquioxides of iron and aluminum and of colloids and overlying a B horizon wherein organic matter and/or sesquioxides of iron have accumulated.

Pole-size—A young tree with a d.b.h. of not less than 10.2 cm (4 in). A small pole has a maximum d.b.h. of 20.3 cm (8 in), and a large pole has a maximum d.b.h. of 30.5 cm (12 in).

Polygamo-dioecious—Bearing perfect and pistillate flowers on female trees and only staminate flowers on male trees.

Polygamous—Plants bearing both perfect and imperfect flowers.

Polymorph—One of several forms of an organism.

Primordium—An organ, a cell, or an organized series of cells in their earliest stage of differentiation, e.g., leaf primordium, sclereid primordium, vessel primordium.

Proembryo—Embryo in early stages of development, often the stages before the main body and suspensor become distinct.

Propagule—A plant part such as a bud, tuber, root, or shoot used to reproduce (propagate) an individual plant vegetatively.

Protandry—The termination of shedding of pollen by a flower prior to the stigma of the same flower being receptive.

Proteranthous—Having flowers appearing before the leaves.

Protogyny—The termination of receptivity prior to the maturation of pollen on the same plant or flower.

Provenance—The original geographic source of seed, pollen, or propagules.

Pumice—A volcanic glass full of cavities and very light in weight.

Pyrene—The pit or seed of a drupe which is surrounded by a bony endocarp.

Pyric—Resulting from, induced by, or associated with burning.

Ramet—An individual member of a clone, derived from an ortet.

Receptivity—The condition of the female flower that permits effective pollination.

Rocky Mountains—In the Forest Service, an area that includes the Dakotas, Nebraska, Kansas, Oklahoma, and Texas west of the 100th meridian, New Mexico, Arizona, Colorado, and the eastern three-quarters of Wyoming.

Saddle—A ridge connecting two higher elevations.

Samara—A dry, indehiscent, winged fruit, one-seeded as in *Fraxinus* and *Ulmus* or two-seeded as in *Acer*.

Sapling—A tree more than 0.9 m (3 ft) in height and less than 10.2 cm (4 in) in d.b.h.

Savannah—Essentially lowland tropical and subtropical grassland, generally with a scattering of trees and/or shrubs. If woody growth is absent it is termed a grass savannah; with shrubs and no trees, a shrub savannah; or with shrubs and widely irregularly scattered trees, a tree savannah.

Scarification (for seed)—Pregerminative treatment to make seed coats permeable to water and gases; accomplished usually by mechanical abrasion or by soaking seeds briefly in a strong acid or other chemical solution.

Schist—A metamorphic crystalline rock having a closely foliated structure divisible along approximately parallel planes.

Scion—An aerial plant part, often a branchlet, that is grafted onto the root-bearing part of another plant.

Sclerenchyma—A protective or supporting tissue in higher plants composed of cells with walls thickened and lignified and often mineralized.

Sedimentary—Formed by or from deposits of sediment.

Seed coat (testa)—The outer coat of the seed derived from the integument(s).

Seedling—A tree grown from seed that has not yet reached a height of 0.9 m (3 ft) or exceeded 5.1 cm (2 in) in d.b.h., which would qualify it as a sapling.

Seed tree—The cutting method that describes the silvicultural system in which the dominant feature is the removal of all trees except for a small number of seed bearers left singly or in small groups, usually 20 to 25 per hectare (8 to 10 per acre). The seed trees are generally harvested when regeneration is established. An even-age stand results.

Selection—*See* **Group selection** and **Individual tree selection.**

Self-pruning—*See* **Natural pruning.**

Selfing (self pollination)—The pollination of an individual or biotype with its own pollen, the offspring being termed selfs.

Sere—A sequence of plant communities that successively follow one another in the same habitat from the pioneer stage to a mesic climax.

Serotinous—Late in developing; particularly applied to plants that flower or fruit late in the season and to fruit and cones that remain closed for a year or more after the seeds mature, but also to bud opening, leaf shedding, etc.

Serpentine—A mineral or rock consisting essentially of a hydrous magnesium silicate. It usually has a dull green color and often a mottled appearance.

Serpentinite—A rock consisting almost wholly of serpentine minerals derived from the alteration of previously existing divine and pyroxene.

Sessile—Without a stalk; sitting directly on its base.

Shade-tolerance classes—Very intolerant, intolerant, intermediate, tolerant, very tolerant.

Shelterwood—The cutting method that describes the silvicultural system in which, in order to provide a source of seed and/or protection for regeneration, the old crop (the shelterwood) is removed in two or more successive shelterwood cuttings. The first cutting is ordinarily the seed cutting, though it may be preceded by a preparatory cutting, and the last is the final cutting. Any intervening cutting is termed a removal cutting. An even-age stand results.

Sialic—Light rock rich in silica and alumina, and typical of the outer layer of the earth.

Silvicultural system—A process whereby forests are tended, harvested, and replaced, resulting in a forest of distinctive form. Systems are classified according to the method of carrying out the fellings that remove the mature crop with a view to regeneration and according to the type of forest thereby produced. These are individual tree selection, group selection, shelterwood, seed tree, and clearcut.

Site class—A measure of the relative productive capacity of a site based upon the volume or height (dominant, codominate, or mean) or the maximum mean annual increment of a stand that is attained or attainable at a given age.

Site index (SI)—A measure of site class based upon the height of the dominant trees in a stand at an arbitrarily chosen age, most commonly at 50 years in the East and 100 years in the West.

Skep—A woven straw beehive.

Soil orders—The 10 soil orders used by the Soil Conservation Service of the USDA in their basic system of soil classification are: Alfisol, Aridisol, Entisol, Histosol, Inceptisol, Mollisol, Oxisol, Spodosol, Ultisol, and Vertisol.

Solum—The upper and most weathered part of the soil profile, i.e., the A and B horizons.

Southeastern—In the Forest Service, an area that includes Virginia, the Carolinas, Georgia, and Florida.

Southern—In the Forest Service, an area that includes Alabama, Tennessee, Mississippi, Arkansas, Louisiana, and Oklahoma and Texas east of the 100th meridian.

Southern pines—Within the United States, the 10 species of hard pines with major portions of their ranges below the Mason-Dixon line, i.e., longleaf, shortleaf, slash, loblolly, spruce, Virginia, sand, pitch, Table Mountain, and pond pine.

Sporangium—A hollow, unicellular or multicellular saclike, spore-producing structure.

Sporophyll—A modified leaf or leaflike structure which bears sporangia, e.g., the stamens and carpels of the angiosperms.

Staminate—Having pollen-bearing organs (stamens) only. May apply to individual male plants of a dioecious species or to flowers, inflorescences, or strobili.

Stand density—A measure of the degree of crowding of trees within stocked areas, commonly expressed by various growing-space ratios such as crown length to tree height, crown diameter to diameter at breast height (1.37 m or 4.5 ft above the ground) (d.b.h.); crown diameter to tree height; or of stem (triangular) spacing to tree height.

Stemflow—Precipitation that is intercepted by vegetative cover and runs down the stem or major axes of such cover.

Steppe—Arid land with xerophilous vegetation usually found in regions of extreme temperature range and loess soil.

Stereome—A collective physiological term for all supporting tissues in a plant, such as sclerenchyma and collenchyma.

Sterigma—A peg-shaped projection to which the leaves of some conifers (as spruces) are attached on the twigs.

Stigma—The part of the pistil, usually the tip, often sticky, which receives the pollen and upon which the pollen germinates.

Stipe—A supporting stalk, such as the stalk of a pistil, a gill fungus, or the petiole of a fern leaf.

Stipule—A small structure or appendage found at the base of some leaf petioles, usually present in pairs. They are morphologically variable and appear as scales, spines, glands, or leaflike structures.

Stoma—A pore in the epidermis and the two guard cells surrounding it. Sometimes applied only to the pore.

Stool—A living stump capable of producing sprouts.

Stratification—A pregerminative treatment to break dormancy in seeds and to promote rapid uniform germination accomplished by exposing seeds for a specified time to moisture at near-freezing temperature sometimes with a preceding exposure to moisture at room temperature.

Strobilus—The male or female fruiting body of the gymnosperms.

Style—The stalk of a pistil which connects the stigma with the ovary.

Suppressed (a crown class)—Very slowly growing trees with crowns in the lower layer of the canopy and leading shoots not free. Such trees are subordinate to dominants, codominants, and intermediates in the crown canopy.

Sympatric—Species or populations inhabiting the same or overlapping areas. *Cf.* **Allopatric.**

Sympodial—A branching growth pattern in which the main axis is formed by a series of successive secondary axes, each of which represents one fork of a dichotomy.

Taungya method—The raising of a forest crop in conjunction with a temporary agricultural crop.

Taxon—Any formal taxonomic group such as genus, species, or variety.

Tepal—Perianth parts undifferentiated into distinct sepals and petals.

Terpene—Any of various isometric hydrocarbons found especially in essential oils (as from conifers), resins, and balsams.

Testa—The outer coat of the seed derived from the integument(s).

Tetraploid (polyploid)—A cell, tissue, or organism having four sets of chromosomes.

Thermic soil temperature—The mean annual soil temperature is 15° C (59° F) or higher but lower than 22° C (72° C), and the difference between mean summer and mean winter soil temperature is more than 5° C (9° F) at a depth of 50 cm (20 in).

Throughfall—All the precipitation reaching the forest floor minus the stemflow, i.e., canopy drip plus direct precipitation.

Top-to-root ratio or root-to-shoot ratio—The relative weights or volumes of the epicotyl and the hypocotyl of a tree seedling, expressed as a ratio.

Tracheid—An elongated, thick-walled, nonliving conducting and supporting cell found in the xylem of most vascular plants.

Triploid—A cell, tissue, or organism having three sets of chromosomes.

T.S.I. (timber stand improvement)—A loose term comprising all intermediate treatments made to improve the composition, constitution, condition, and increment of a timber stand.

Tuff—A rock composed of the finer kinds of volcanic detritus usually fused together by heat.

Umbo—A blunt or rounded projection arising from a surface, as on a pine cone scale.

Uneven-aged—A condition of forest or stand that contains intermingled trees that differ markedly in age. By convention, a minimum range of 10 to 20 years is generally accepted, though with rotations of not less than 100 years, 25 percent (USA) of the rotation may be the minimum.

Variety—A subdivision of a species, usually separated geographically from the typical, having one or more heritable, morphological characteristics which differ from the typical even when grown under the same environmental conditions; a morphological variant.

Xerophyte—A plant that is adapted to dry or arid habitats.

Summary of Tree Characteristics

Russell M. Burns and Barbara H. Honkala[1]

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	Scientific name				
Ailanthus	*Ailanthus altissima* (Mill.) Swingle	Intolerant	D	E	U, I, E
Alaska-cedar	*Chamaecyparis nootkatensis* (D. Don) Spach	Tolerant	M	E	H, S
Alpine larch	*Larix lyallii* Parl.	Very intolerant	M	E	E, I
American basswood	*Tilia americana* L.	Tolerant	Perfect	E	AL, I, S
American beech	*Fagus grandifolia* Ehrh.	Very tolerant	M	E	AL, O, S
American elm	*Ulmus americana* L.	Intermediate	Perfect	E	AL, I, M, U
American holly	*Ilex opaca* Ait.	Very tolerant	D	E	I, U
American hornbeam	*Carpinus caroliniana* Walt.	Very tolerant	M	E	AL, U, I, E, S, H, M
Atlantic white-cedar	*Chamaecyparis thyoides* (L.) B.S.P.	Intermediate	M	E	S, H
Ausubo	*Manilkara bidentata* (A. DC.) Chev.	Very tolerant	Perfect	E	I, O
Baldcypress	*Taxodium distichum* (L.) Rich. var. *distichum*	Intermediate	M	E	S, U, I, AL, E
Balsam fir	*Abies balsamea* (L.) Mill.	Very tolerant	M	E	S, I, H
Balsam poplar	*Populus balsamifera* L.	Very intolerant	D	E	I, E
Bigcone Douglas-fir	*Pseudotsuga macrocarpa* (Vasey) Mayr	Intolerant	M	E	I, AL
Bigleaf maple	*Acer macrophyllum* Pursh	Very tolerant	Polygamous	E	I, U, S, M, E, AL
Bigtooth aspen	*Populus grandidentata* Michx.	Very intolerant	D	E	S, AL, I
Bitternut hickory	*Carya cordiformis* (Wangenh.) K. Koch	Intolerant	M	H	U, I, M, AL
Black ash	*Fraxinus nigra* Marsh.	Intolerant	Polygamous	E	H, E
Black cherry	*Prunus serotina* Ehrh.	Intolerant	Perfect	H	I, U, AL
Black cottonwood	*Populus trichocarpa* Torr. & Gray	Very intolerant	D	E	E, I
Black locust	*Robinia pseudoacacia* L.	Very intolerant	Perfect	E	I, U, AL
Black maple	*Acer nigrum* Michx. f.	Very intolerant	Polygamous	E	M, I, E, S
Black oak	*Quercus velutina* Lam.	Intermediate	M	H	S, AL, M, U, E, I
Black spruce	*Picea mariana* (Mill.) B.S.P.	Tolerant	M	E	H, S, I, E
Black tupelo	*Nyssa sylvatica* Marsh. var. *sylvatica*	Tolerant	Plygamo-D	E	U
Black walnut	*Juglans nigra* L.	Intolerant	M	H	AL, E
Black willow	*Salix nigra* Marsh.	Very intolerant	D	E	E
Blue oak	*Quercus douglasii* Hook. & Arn.	Intolerant	M	H	AL, I, M
Blue spruce	*Picea pungens* Engelm.	Intermediate	M	E	M, H, I
Bluegum eucalyptus	*Eucalyptus globulus* Labill.	Intolerant	Perfect	E	U, AL, I, AR
Boxelder	*Acer negundo* L.	Tolerant	D	E	E, I, AL, U, M
Brewer spruce	*Picea breweriana* Wats.	Tolerant	M	E	E
Bur oak	*Quercus macrocarpa* Michx.	Intermediate	M	H	AL, M, S
Butternut	*Juglans cinerea* L.	Intolerant	M	H	AL, E
Cabbage palmetto	*Sabal palmetto* (Walt.) Lodd. ex J. A. & J. H. Schult.	Tolerant	Perfect	H	E, AL, U, S
California black oak	*Quercus kelloggii* Newb.	Intolerant	M	H	AL, I, M
California-laurel	*Umbellularia californica* (Hook. & Arn.) Nutt.	Tolerant	Perfect	H	I, M, U
California red fir	*Abies magnifica* A. Murr.	Tolerant	M	E	E, I, AL, S
Canyon live oak	*Quercus chrysolepis* Liebm.	Tolerant	M	H	I, AL
Carolina silverbell	*Halesia carolina* L.	Tolerant	Perfect	E	U, E, I, M
Casuarina	*Casuarina* spp.	Intolerant	M, D	E	E, I, S
Cedar elm	*Ulmus crassifolia* Nutt.	Intermediate	Perfect	E	I, V
Cedro hembra	*Cedrela odorata* L.	Intolerant	Perfect	E	U

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[1] The authors are Principal Silviculturist and Botanist (retired), Timber Management Research, Washington, DC.

[2] Flowering: M = Monoecious, D = Dioecious.

[3] Soil Orders: AL = Alfisols, AR = Aridisols, E = Entisols, H = Histosols, I = Inceptisols, M = Mollisols, O = Oxisols, S = Spodosols, U = Ultisols, V = Vertisols.

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	**Scientific name**				
Cherrybark oak	*Quercus falcata* var. *pagodifolia* Ell.	Intolerant	M	H	AL, I
Chestnut oak	*Quercus prinus* L.	Intermediate	M	H	U, I
Chinkapin oak	*Quercus muehlenbergii* Engelm.	Intolerant	M	H	AL, I, M, U
Common persimmon	*Diospyros virginiana* L.	Very tolerant	D	E	AL, U, E, I
Corkbark fir	*Abies lasiocarpa var. arizonica* (Merriam) Lemm.	Tolerant	M	E	I, E, AL
Cucumbertree	*Magnolia acuminata* L.	Intermediate	Perfect	E	I, U
Digger pine	*Pinus sabiniana* Dougl.	Very intolerant	M	E	AL, E, I, M, U
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco	Intermediate	M	E	I, S, AL, M, E, U
Eastern cottonwood	*Populus deltoides* Bartr. ex Marsh. var. *deltoides*	Very intolerant	D	E	E, I
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	Very tolerant	M	E	S
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	Tolerant	M	E	S, AL, M, U, E, I
Eastern redbud	*Cercis canadensis* L.	Tolerant	Perfect	E	AL, M
Eastern redcedar	*Juniperus virginiana* L.	Intol.-Very Intol.	D	E	M, U
Eastern white pine	*Pinus strobus* L.	Intermediate	M	E	I, U, S, E, AL
Engelmann spruce	*Picea engelmannii* Parry ex Engelm.	Tolerant	M	E	I, E, AL, H
Eucalyptus grandis	*Eucalyptus grandis* Hile ex Maiden	Very Intolerant	Perfect	E	S
European alder	*Alnus glutinosa* (L.) Gaertn.	Intolerant	M	E	H, I, E
European black pine	*Pinus nigra* Arnold	Intolerant	M	E	AR, E, M, V
Florida maple	*Acer barbatum* Michx.	Tolerant	Polygamo-D	E	I, E, U
Florida torreya	*Torreya taxifolia* Arn.	Tolerant	D	H	AL, M
Flowering dogwood	*Cornus florida* L.	Very tolerant	Perfect	E	U, I, AL, S, E
Fraser fir	*Abies fraseri* (Pursh) Poir.	Very tolerant	M	E	I
Fraser magnolia	*Magnolia fraseri* Walt.	Intermediate	Perfect	E	I, U
Giant chinkapin	*Castanopsis chrysophylla* (Dougl.) A. DC.	Intermediate	M	H	I, E, U, AL
Giant sequoia	*Sequoiadendron giganteum* (Lindl.) Buchholz	Intolerant	M	E	I, AL
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.	Tolerant	M	E	S
Green ash	*Fraxinus pennsylvanica* Marsh.	Tolerant	D	E	I, E
Hackberry	*Celtis occidentalis* L.	Intermediate	Polygamo-M	E	M, E, I
Honeylocust	*Gleditsia triacanthos* L.	Intolerant	Polygamo-D	E	AL, I, M
Incense-cedar	*Libocedrus decurrens* Torr.	Intermediate	M	E	AL
Jack pine	*Pinus banksiana* Lamb.	Intolerant	M	E	S, E
Jeffrey pine	*Pinus jeffreyi* Grev. & Balf.	Intolerant	M	E	I, AL, E
Kiawe	*Prosopis pallida* (Humb. & Bonpl. ex Willd.) H.B.K.	Intolerant	Perfect	E	I, M, V
Koa	*Acacia koa* Gray	Intolerant	Perfect	E	I, H, U, O
Laurel	*Cordia alliodora* (Riuz & Pav.) Oken	Intolerant	Perfect	E	E, O, I, U, AL
Laurel oak	*Quercus laurifolia* Michx.	Tolerant	M	H	U, I
Limber pine	*Pinus flexilis* James	Intolerant	M	E	E
Live oak	*Quercus virginiana* Mill.	Intermediate	M	H	U, S, H, E
Loblolly-bay	*Gordonia lasianthus* (L.) Ellis	Tolerant	Perfect	E	S, I, U, H, E, M
Loblolly pine	*Pinus taeda* L.	Intolerant	M	E	U, E, S, AL
Lodgepole pine	*Pinus contorta* Dougl. ex Loud.	Very intolerant	M	E	I, AL, U, H
Longleaf pine	*Pinus palustris* Mill.	Intolerant	M	E	U, E, S
Maria	*Calophyllum calaba* L.	Intermediate	Polygamous	H	I, O, AL
Melaleuca	*Melaleuca quinquenervia* (Cav.) S.T. Blake	Intolerant	Perfect	E	E, S, H, I, U, O
Mockernut hickory	*Carya tomentosa* (Poir.) Nutt.	Intolerant	M	H	U, I, M, AL
Monkey-pod	*Pithecellobium saman* (Jacq.) Benth.	Intolerant	Perfect	E	O, I
Monterey pine	*Pinus radiata* D. Don	Intermediate	M	E	M, U, E, AL
Mountain hemlock	*Tsuga mertensiana* (Bong.) Carr.	Tolerant	M	E	S, E, I, H
Noble fir	*Abies procera* Rehd.	Intermediate	M	E	S, I
Northern red oak	*Quercus rubra* L.	Intermediate	M	H	S, AL, I, M, U, E
Northern white-cedar	*Thuja occidentalis* L.	Tolerant	M	E	H, I, E
Nutmeg hickory	*Carya myristiciformis* (Michx. f.) Nutt.	Intolerant	M	H	AL, I

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	**Scientific name**				
Nuttall oak	*Quercus nuttallii* Palmer	Intolerant	M	H	I, E
Ogeechee tupelo	*Nyssa ogeche* Bartr. ex Marsh.	Intolerant	Polygamo-D	E	I
'Ohi'a lehua	*Metrosideros polymorpha* Gaud.	Intolerant	Perfect	E	H, I, M, S, O, U, AL
Ohio buckeye	*Aesculus glabra* Willd.	Tolerant	Polygamo-M	H	AL
Oregon ash	*Fraxinus latifolia* Benth.	Intermediate	D	E	AL, I, M, U
Oregon white oak	*Quercus garryana* Dougl. ex Hook.	Intolerant	M	H	AL, I, M, U
Osage-orange	*Maclura pomifera* (Raf.) Schneid.	Intolerant	D	E	AL, U, V, M
Overcup oak	*Quercus lyrata* Walt.	Intermediate	M	H	I, AL
Pacific madrone	*Arbutus menziesii* Pursh	Intermediate	Perfect	E	AL, U, I
Pacific silver fir	*Abies amabilis* Dougl. ex Forbes	Very tolerant	M	E	H, E, I, S
Pacific yew	*Taxus brevifolia* Nutt.	Very tolerant	D	E	U, AL, I
Paper birch	*Betula papyrifera* Marsh.	Intolerant	M	E	S, I
Pecan	*Carya illinoensis* (Wangenh.) K. Koch	Intolerant	M	H	E, I, AL
Pignut hickory	*Carya glabra* (Mill.) Sweet	Intermediate	M	H	U, AL, M
Pin cherry	*Prunus pensylvanica* L.	Very intolerant	Perfect	E	I, S, AL, H, E, M
Pin oak	*Quercus palustris* Muenchh.	Intolerant	M	H	E, AL
Pinyon	*Pinus edulis* Engelm.	Intolerant	M	E	AL, I
Pitch pine	*Pinus rigida* Mill.	Intolerant	M	E	S, AL, E, U
Plains cottonwood	*Populus deltoides* var. *occidentalis* Rydb.	Very intolerant	D	E	E, M, AL, I
Pondcypress	*Taxodium distichum* var. *nutans* (Ait.) Sweet	Intermediate	M	E	S, U
Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws.	Intolerant	M	E	E, I, M, AL, U
Pond pine	*Pinus serotina* Michx.	Intolerant	M	E	U
Poplar hybrids	*Populus* spp.	Very intolerant	D	E	E, I, M, S, U
Port-Orford-cedar	*Chamaecyparis lawsoniana* (A. Murr.) Parl.	Tolerant	M	E	S, U, I
Post oak	*Quercus stellata* Wangenh.	Intolerant	M	H	U, AL
Pumpkin ash	*Fraxinus profunda* (Bush) Bush	Intermediate	D	E	AL, E, S, U
Quaking aspen	*Populus tremuloides* Michx.	Very intolerant	D, Perfect	E	AL, S, I, H
Red alder	*Alnus rubra* Bong.	Intolerant	M	E	I, E, AL, U, H
Redbay	*Persea borbonia* (L.) Spreng.	Tolerant	Perfect	H	H
Red maple	*Acer rubrum* L.	Tolerant	Polygamo-D	E	E, I, U, AL, S, H
Red mulberry	*Morus rubra* L.	Tolerant	M, D	E	AL, I, S, U
Red pine	*Pinus resinosa* Ait.	Intolerant	M	E	E, S, AL, I
Red spruce	*Picea rubens* Sarg.	Toler.-Very Toler.	M	E	S, I, H
Redwood	*Sequoia sempervirens* (D. Don) Endl.	Very tolerant	M	E	I, U
River birch	*Betula nigra* L.	Intolerant	M	E	E
Roble blanco	*Tabebuia heterophylla* (DC.) Britton	Intolerant	Perfect	E	I
Robusta eucalyptus	*Eucalyptus robusta* Sm.	Intolerant	Perfect	E	O, U, H, I
Rock elm	*Ulmus thomasii* Sarg.	Intermediate	Perfect	E	M, AL, S
Rocky Mountain juniper	*Juniperus scopulorum* Sarg.	Very intolerant	D	E	M
Rosegum eucalyptus	*Eucalyptus grandis* Hill ex Maiden	Very intolerant	Perfect	E	S
Royal paulownia	*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.	Intolerant	Perfect	E	AL
Saligna eucalyptus	*Eucalyptus saligna* Sm.	Very intolerant	Perfect	E	H, I, O, U
Sand pine	*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.	Intermediate	M	E	E
Sassafras	*Sassafras albidum* (Nutt.) Nees	Intolerant	D	H	E, AL, U
Scarlet oak	*Quercus coccinea* Muenchh.	Very intolerant	M	H	AL, I, U
Scotch pine	*Pinus sylvestris* L.	Intolerant	M (mostly)	E	S, E, I, H, AL, M
September elm	*Ulmus serotina* Sarg.	Tolerant	Perfect	E	U, AL, I
Shagbark hickory	*Carya ovata* (Mill.) K. Koch	Intermediate	M	H	U, AL, M
Shellbark hickory	*Carya laciniosa* (Michx. f.) Loud.	Very tolerant	M	H	AL
Shortleaf pine	*Pinus echinata* Mill.	Intolerant	M	E	U
Shumard oak	*Quercus shumardii* Buckl.	Intolerant	M	H	AL, I, V
Silk-oak	*Grevillea robusta* A. Cunn.	Very intolerant	Perfect	E	H, I, U
Silver maple	*Acer saccharinum* L.	Tolerant	Polygamous	E, H	S, I, M, H
Singleleaf pinyon	*Pinus monophylla* Torr. & Frem.	Intolerant	M	E	M

Tree species					
Common name	**Scientific name**	**Shade tolerance class**	**Flowering characteristic^2**	**Germination, epigeal or hypogeal**	**Most common soil orders^3**
Sitka spruce	*Picea sitchensis* (Bong.) Carr.	Tolerant	M	E	E, S, I, H
Slash pine	*Pinus elliottii* Engelm.	Intolerant	M	E	S, U, E
Slippery elm	*Ulmus rubra* Muhl.	Tolerant	Perfect	E	M, AL
Sourwood	*Oxydendrum arboreum* (L.) DC.	Tolerant	Perfect	E	U, I, E
Southern magnolia	*Magnolia grandiflora* L.	Tolerant	Perfect	E	S, AL, V, U
Southern redcedar	*Juniperus silicicola* (Small) Bailey	Intol.-Very intol.	D	E	AL, E, I, S, U
Southern red oak	*Quercus falcata* Michx. var. *falcata*	Intermediate	M	H	U, AL
Spruce pine	*Pinus glabra* Walt.	Very tolerant	M	E	S, E
Striped maple	*Acer pensylvanicum* L.	Very tolerant	M, D	E	I, AL, S, M
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.	Tolerant	M	E	I, E, AL
Sugarberry	*Celtis laevigata* Willd.	Tolerant	Polygamo-M	E	I, E
Sugar maple	*Acer saccharum* Marsh.	Very tolerant	Polygamous	E	S, AL, M
Sugar pine	*Pinus lambertiana* Dougl.	Intermediate	M	E	U, AL
Swamp chestnut oak	*Quercus michauxii* Nutt.	Intolerant	M	H	AL, I
Swamp cottonwood	*Populus heterophylla* L.	Intolerant	D	E	AL, I, E
Swamp tupelo	*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.	Intolerant	Polygamo-D	E	U, I, E
Swamp white oak	*Quercus bicolor* Willd.	Intermediate	M	H	E, I
Sweetbay	*Magnolia virginiana* L.	Intermediate	Perfect	E	U, S, H
Sweet birch	*Betula lenta* L.	Intolerant	M	E	S, I, U
Sweetgum	*Liquidambar styraciflua* L.	Intolerant	M	E	AL
Sycamore	*Platanus occidentalis* L.	Intermediate	M	E	E, I, AL, V, H, M
Table Mountain pine	*Pinus pungens* Lamb.	Intolerant	M	E	I
Tabonuco	*Dacryodes excelsa* Vahl	Intermediate	D	E	U
Tamarack	*Larix laricina* (Du Roi) K. Koch	Very intolerant	M	E	H, I, E
Tanoak	*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.	Tolerant	M	H	I, AL
Turkey oak	*Quercus laevis* Walt.	Intolerant	M	H	E
Virginia pine	*Pinus virginiana* Mill.	Intolerant	M	E	S, I
Water hickory	*Carya aquatica* (Michx. f.) Nutt.	Intermediate	M	H	I
Water oak	*Quercus nigra* L.	Intolerant	M	H	I
Water tupelo	*Nyssa aquatica* L.	Intolerant	Polygamo-D	E	AL, E, H, I
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.	Very tolerant	M	E	AL, E, H, I, S, U
Western juniper	*Juniperus occidentalis* Hook.	Intolerant	M	E	M, AR, E, V
Western larch	*Larix occidentalis* Nutt.	Very intolerant	M	E	I, AL, S
Western redcedar	*Thuja plicata* Donn ex D. Don	Very tolerant	M	E	I, U, H
Western white pine	*Pinus monticola* Dougl. ex D. Don	Intermediate	M	E	S
White ash	*Fraxinus americana* L.	Intolerant	D	E	AL, S, I
White basswood	*Tilia heterophylla* Vent.	Tolerant	Perfect	E	I, U, AL, E, M
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	Tolerant	M	E	I, E, AL, U
White oak	*Quercus alba* L.	Intermediate	M	H	AL, U
White spruce	*Picea glauca* (Moench) Voss	Intermediate	M	E	AL, I
Whitebark pine	*Pinus albicaulis* Engelm.	Intermediate	M	E	I, E, M
Willow oak	*Quercus phellos* L.	Intolerant	M	H	I, AL
Winged elm	*Ulmus alata* Michx.	Tolerant	Perfect	E	AL, U
Yagrumo hembra	*Cecropia peltata* L.	Intolerant	D	E	U, M, AL, O, I
Yagrumo macho	*Didymopanax morototoni* (Aubl.) Decne. & Planch.	Intolerant	Perfect	E	E, U, I, M
Yellow birch	*Betula alleghaniensis* Britton	Intermediate	M	E	S, I, AL
Yellow buckeye	*Aesculus octandra* Marsh.	Tolerant	Polygamo-M	H	AL, E
Yellow-poplar	*Liriodendron tulipifera* L.	Intolerant	Perfect	E	I, U

Checklist of Insects and Mites

Scientific name	Common name[1]
Abebaea cervella Walsingham	(a leafroller moth)
Abgrallaspis ithacae (Ferris)	hemlock scale
Acantholyda erythrocephala (Linnaeus)	pine false webworm
Acantholyda pini Rohwer	(a web-spinning sawfly)
Acantholyda zappei (Rohwer)	(nesting-pine sawfly)
Acleris chalybeana (Fernald)	(a leafroller moth)
Acleris gloverana (Walsingham)	western blackheaded budworm
Acrobasis betulella Hulst	birch tubemaker
Acrobasis caryivorella Ragonot	(a casebearer)
Acrobasis demotella Grote	walnut shoot moth
Acrobasis juglandis (LeBaron)	pecan leaf casebearer
Acronicta americana (Harris)	American dagger moth
Acronicta lepusculina Guenee	cottonwood dagger moth
Actias luna (Linnaeus)	luna moth
Adelges abietis (Linnaeus)	eastern spruce gall adelgid
Adelges cooleyi (Gillette)	Cooley spruce gall adelgid
Adelges nordmannianae (Eckstein)	(a gall)
Adelges nusslini (Borner)	(a woolly aphid)
Adelges piceae (Ratzeburg)	balsam woolly adelgid
Aethes rutilana (Hubner)	pale juniper webworm
Agrilus acutipennis Mannerheim	(a flatheaded borer)
Agrilus angelicus Horn	(Pacific oak twig girdler)
Agrilus anxius Gory	bronze birch borer
Agrilus arcuatus torquatus LeConte	(hickory spiral borer)
Agrilus bilineatus (Weber)	twolined chestnut borer
Agrilus burkei Fisher	(a flatheaded borer)
Agrilus cephalicus LeConte	(a flatheaded borer)
Agrilus difficilis Gory	(a flatheaded borer)
Agrilus fuscipennis Gory	(a flatheaded borer)
Agrilus horni Kerremans	(a flatheaded borer)
Agrilus liragus Barter & Brown	bronze poplar borer
Agrilus otiosus Say	(a flatheaded borer)
Agrilus politus (Say)	(a flatheaded borer)
Agromyza albitarsis Meigen	(a leafminer fly)
Aleuroplatus coronatus (Quaintance)	(crown whitefly)
Alniphagus aspericollis (LeConte)	alder bark beetle
Alsophila pometaria (Harris)	fall cankerworm
Altica ambiens LeConte	alder flea beetle
Amblycerus robiniae (Fabricius)	(a seed beetle)
Amphibolips confluenta (Harris)	large oak-apple wasp
Amphicerus bicaudatus (Say)	apple twig borer
Anacampsis niveopulvella (Chambers)	(a gelechiid moth)
Anacamptodes pergacilis (Hulst)	(a looper)
Andricus quercuscalifornicus (Bassett)	(a gall wasp)
Aneflormorpha subpubescens (LeConte)	(oak stem borer)
Anisococcus crawi (Coquillett)	(white sage mealybug)
Anisota rubicunda (Fabricius)	(green-striped mapleworm)
Anisota senatoria (J. E. Smith)	orangestriped oakworm
Anisota stigma (Fabricius)	spiny oakworm
Anisota virginiensis (Drury)	pinkstriped oakworm
Anomala oblivia Horn	pine chafer
Anoplonyx laricivorus (Rohwer & Middleton)	(twolined larch sawfly)
Anoplonyx occidens Ross	(western larch sawfly)
Anthaxia aeneogaster Laporte & Gory	(a flatheaded twig borer)
Antispila nysaefoliella Clemens	tupelo leafminer
Antron douglasii (Ashmead)	(spined turban gall)
Aphis gossypii Glover	cotton aphid, melon aphid
Aphis maculatae (Fitch)	(spotted poplar aphid)
Aphrophora parallela (Say)	pine spittlebug
Aphrophora saratogensis (Fitch)	Saratoga spittlebug
Apteromechus ferratus (Say)	(a wood-boring weevil)
Araecerus levipennis Jordan	koa haole seed weevil
Archips argyrospila (Walker)	fruittree leafroller
Archips fervidana (Clemens)	oak webworm
Archips negundana (Dyar)	(a leafroller)
Archodontes melanopus (Linnaeus)	(a roundheaded borer)
Argyresthia laricella Kearfott	(larch shoot moth)
Argyresthia thuiella (Packard)	arborvitae leafminer
Argyrotaenia juglandana (Fernald)	hickory leafroller
Argyrotaenia pinatubana (Kearfott)	pine tube moth
Argyrotaenia quercifoliana (Fitch)	(a leaf roller)
Argyrotaenia tabulana Freeman	(lodgepole needletier)
Arrhenodes minutus (Drury)	oak timberworm
Artipus floridanus Horn	(leaf notcher weevil)
Ascalapha odorata (Linnaeus)	black witch
Asphondylia ilicicola Foote	(a gall midge)
Asterocampa celtis (Boisduval & LeConte)	(hackberry butterfly)
Asterolecanium minus Lindinger	(a pit scale)
Asterolecanium pustulans (Cockerell)	oleander pit scale
Asterolecanium puteanum Russell	(holly pit scale)
Asterolecanium quercicola (Bouché)	(a pit scale)
Asterolecanium variolosum (Ratzeburg)	golden oak scale
Atimia confusa dorsalis LeConte	(a roundheaded borer)
Atimia confusa maritima Linsley	(a roundheaded borer)
Atimia huachucae Champlain and Knull	(a roundheaded borer)
Atimia vandykei Linsley	(a roundheaded borer)
Atta texana (Buckley)	Texas leafcutting ant
Atteva punctella (Cramer)	(ailanthus webworm)
Augomonoctenus libocedrii Rohwer	(incense-cedar cone sawfly)
Automeris io (Fabricius)	io moth
Azteca alfari Emery	(an ant)
Azteca constructor Emery	(an ant)
Baliosus ruber Weber	basswood leafminer
Barbara colfaxiana (Kearfott)	Douglas-fir cone moth

Scientific name	Common name[1]
Barbara mappana Freeman	(cone moth)
Bassettia ligni Kinsey	(a gall wasp)
Besbicus mirabilis (Kinsey)	(a gall wasp)
Bucculatrix albertiella Busck	(oak ribbedcase maker)
Bucculatrix canadensisella Chambers	birch skeletonizer
Bucculatrix recognita Braun	(an oak skeletonizer)
Buprestis aurulenta Linnaeus	golden buprestid
Caliroa lineata MacGillivary	(pin oak sawfly)
Caliroa quercuscoccineae Dyar	scarlet oak sawfly
Callidium hoppingi Linsley	(a roundheaded borer)
Callidium juniperi Fisher	(a roundheaded borer)
Callidium texanum Schaeffer	(a roundheaded borer)
Calligrapha scalaris (LeConte)	elm calligrapha
Callirhopalus bifasciatus (Roelofs)	(Japanese weevil)
Callirhytis cornigera (Osten Sacken)	(horned oak gall)
Callirhytis perdens (Kinsey)	(a gall wasp)
Callirhytis quercuspunctata (Bassett)	(gouty oak gall)
Caloptilia negundella (Chambers)	(boxelder leafroller)
Cameraria umbellulariae (Walsingham)	(a leafblotch miner)
Camponotus ferrugineus (Fabricius)	red carpenter ant
Camponotus pennsylvanicus (De Geer)	black carpenter ant
Canarsia ulmiarrosorella (Clem.)	(a pyralid moth)
Carulaspis juniperi (Bouche)	juniper scale
Carynota stupida (Walker)	(a treehopper)
Caryobruchus gleditsiae (Linnaeus)	(a seed beetle)
Caryomyia holotricha (Osten Sacken)	(a gall midge)
Caryomyia sanguinolenta (Osten Sacken)	(a gall midge)
Caryomyia tubicola (Osten Sacken)	(a gall midge)
Cecidomyia piniinopis Osten Sacken	(gouty pitch midge)
Cecidomyia reeksi Vockeroth	(a gall midge)
Ceratomia undulosa (Walker)	(a sphinx moth)
Ceresium unicolor (Fabricius)	(a roundheaded borer)
Chaitophorus populicola (Thomas)	(an aphid)
Chalcophorella campestris (Say)	(flatheaded sycamore-heartwood borer)
Chionaspis americana Johnson	elm scurfy scale
Chionaspis corni Cooley	dogwood scale
Chionaspis lintneri Comstock	(linter scale)
Chionaspis pinifoliae (Fitch)	pine needle scale
Choristoneura conflictana (Walker)	large aspen tortrix
Choristoneura fumiferana (Clemens)	spruce budworm
Choristoneura lambertiana (Busck)	(sugar pine tortrix)
Choristoneura occidentalis Freeman	western spruce budworm
Choristoneura pinus Freeman	jack pine budworm
Choristoneura retiniana (Walsingham)	(modoc budworm)
Choristoneura rosaceana (Harris)	obliquebanded leafroller
Chrysobothris azurea LeConte	(a flatheaded borer)
Chrysobothris femorata (Olivier)	flatheaded appletree borer
Chrysobothris mali Horn	Pacific flatheaded borer
Chrysobothris nixa Horn	(flatheaded cedar borer)
Chrysobothris sexsignata (Say)	(a flatheaded borer)
Chrysobothris texana LeConte	(a flatheaded borer)
Chrysobothris tranquebarica (Gmelin)	Australian pine borer
Chrysomela crotchi Brown	aspen leaf beetle
Chrysomela scripta Fabricius	cottonwood leaf beetle
Chrysomphalus obscurus	(obscure scale)
Chrysoteuchia topiaria (Zeller)	cranberry girdler
Cimbex americana Leach	elm sawfly
Cinara coloradensis (Gillette)	(black polished spruce aphid)
Cinara fornacula Hottes	green spruce aphid
Cinara sabinae (Gillette & Palmer)	(Rocky Mountain juniper aphid)
Cinara strobi (Fitch)	white pine aphid
Cinara tujafilina (del Guercio)	(an aphid)
Citheronia regalis (Fabricius)	regal moth
Clastoptera undulata Uhler	(a spittlebug)
Cnidocampa flavescens (Walker)	oriental moth
Coleophora laricella (Hubner)	larch casebearer
Coleophora serratella (Linnaeus)	(birch casebearer)
Coleophora ulmifoliella McDunnough	elm casebearer
Coleotechnites edulicola Hodges & Stevens	(pinyon needle miner)
Coleotechnites juniperella (Kearfott)	(a gelechiid moth)
Coleotechnites milleri (Busck)	lodgepole needleminer
Coleotechnites occidentis (Freeman)	(a gelechiid moth)
Coleotechnites piceaella (Kearfott)	(a gelechiid moth)
Coleotechnites thujaella (Kearfott)	(a gelechiid moth)
Colopha ulmicola (Fitch)	elm cockscomb gall aphid
Coloradia pandora Blake	pandora moth
Conophthorus banksianae McPherson	jack pine tip beetle
Conophthorus coniperda (Schwarz)	white pine cone beetle
Conophthorus edulis Hopkins	piñon cone beetle
Conophthorus lambertianae Hopkins	sugar pine cone beetle
Conophthorus monophyllae Hopkins	(single leaf piñon cone beetle)
Conophthorus monticolae Hopkins	mountain pine cone beetle
Conophthorus ponderosae Hopkins	ponderosa pine cone beetle
Conophthorus radiatae Hopkins	Monterey pine cone beetle
Conotrachelus affinis Boheman	(a hickory nut weevil)
Conotrachelus aratus (Germar)	(a snout weevil)
Conotrachelus hicoriae Schoof	(a snout weevil)

Scientific name	Common name[1]
Conotrachelus juglandis LeConte	butternut curculio
Conotrachelus naso LeConte	(a snout weevil)
Conotrachelus posticatus Boheman	(a snout weevil)
Conotrachelus retentus (Say)	black walnut curculio
Contarinia cerasiserotinae (Osten Sacken)	(a gall midge)
Contarinia juniperina Felt	juniper midge
Contarinia negundifolia Felt	(boxelder gall midge)
Contarinia oregonensis Foote	(Douglas-fir cone midge)
Contarinia washingtonensis Johnson	(cone scale midge)
Coptotermes niger Snyder	(a termite moth)
Correbidia terminalis Hampson	(a ctenuchid moth)
Corthylus columbianus Hopkins	Columbian timber beetle
Corythucha aesculi O. & D.	(a lace bug)
Corythucha arcuata (Say)	oak lace bug
Corythucha ciliata (Say)	sycamore lace bug
Corythucha juglandis (Fitch)	(a walnut lace bug)
Corythucha pallipes Parshley	(a birch lace bug)
Cossula magnifica (Strecker)	pecan carpenterworm
Croesia semipurpurana (Kearfott)	oak leaftier
Croesus latitarsus Norton	dusky birch sawfly
Cryptococcus fagisuga Lindinger	beech scale
Cryptophlebia illepida (Butler)	koa seedworm
Cryptorhynchus lapathi (Linnaeus)	poplar-and-willow borer
Cryptotermes brevis (Walker)	West Indian drywood termite
Cudonigera houstonana (Grote)	(a budworm moth)
Curculio caryae (Horn)	pecan weevil
Curculio longidens (Chittenden)	(a snout weevil)
Curculio pardalis Chittenden	(a snout weevil)
Curculio sulcatulus (Casey)	(a snout weevil)
Curculio uniformis (LeConte)	filbert weevil
Cylindrocopturus eatoni Buchanan	(pine reproduction weevil)
Cyrtepistomus castaneus (Roelofs)	Asiatic oak weevil
Dasineura balsamicola (Lintner)	(balsam gall midge)
Dasineura rachiphaga Tripp	(spruce cone axis midge)
Dasychira basiflava (Packard)	(dark tussock moth)
Datana integerrima Grote & Robinson	walnut caterpillar
Datana ministra (Drury)	yellownecked caterpillar
Dendrocoris pini Montandon	(a stink bug)
Dendroctonus adjunctus Blandford	roundheaded pine beetle
Dendroctonus approximatus Dietz	Mexican pine beetle
Dendroctonus brevicomis LeConte	western pine beetle
Dendroctonus frontalis Zimmermann	southern pine beetle
Dendroctonus jeffreyi Hopkins	Jeffrey pine beetle
Dendroctonus ponderosae Hopkins	mountain pine beetle
Dendroctonus pseudotsugae Hopkins	Douglas-fir beetle

Scientific name	Common name[1]
Dendroctonus rufipennis (Kirby)	spruce beetle
Dendroctonus simplex LeConte	eastern larch beetle
Dendroctonus terebrans (Olivier)	black turpentine beetle
Dendroctonus valens LeConte	red turpentine beetle
Derocrepis aesculi (Drury)	(a flea beetle)
Desmia funeralis (Hubner)	grape leaffolder
Diapheromera femorata (Say)	walkingstick
Diaphnocoris chlorionis (Say)	honeylocust plant bug
Dicerca divaricata (Say)	(a flatheaded borer)
Dicerca lurida (Fabricius)	(a flatheaded borer)
Dicerca tenebrica (Kirby)	(a flatheaded borer)
Dichelonyx valida LeConte	(a scarab beetle)
Dichomeris marginella (Fabricius)	juniper webworm
Dictyla montropidia (Stal)	(Spanish elm lacewing bug)
Dioryctria abietivorella (Grote)	(fir coneworm)
Dioryctria albovittella (Hulst)	(a coneworm)
Dioryctria amatella (Hulst)	southern pine coneworm
Dioryctria pygmaeella Ragonot	baldcypress coneworm
Dioryctria reniculelloides Mutuura & Munroe	spruce coneworm
Dioryctria resinosella Mutuura	red pine shoot moth
Dioryctria yatesi Mutuura & Munroe	(mountain pine coneworm)
Dioryctria zimmermani (Grote)	Zimmerman pine moth
Diplotaxis sordida (Say)	(a scarab beetle)
Diprion frutetorum Fabricius	(a sawfly)
Diprion similis (Hartig)	introduced pine sawfly
Dorcaschema alternatum (Say)	(a roundheaded borer)
Dorcaschema wildii Uhler	(mulberry borer)
Dryocoetes affaber (Mannerheim)	(a bark beetle)
Dryocoetes betulae Hopkins	birch bark beetle
Dryocoetes confusus Swaine	western balsam bark beetle
Dysmicoccus wistariae Green	(a mealybug)
Earomyia abietum McAlpine	(fir seed maggot)
Earomyia barbara McAlpine	(a cone maggot)
Earomyia longistylata McAlpine	(a cone maggot)
Ecdytolopha insiticiana Zeller	locust twig borer
Ectropis crepuscularia (D. & S.)	(saddleback looper)
Elaphidionoides villosus (Fabricius)	(twig pruner)
Elasmuche lateralis (Say)	(a stink bug)
Elatobium abietinum (Walker)	spruce aphid
Empoasca pergandei Gillette	(a leafhopper)
Enaphalodes rufulus (Haldeman)	red oak borer
Ennomos magnaria Guenee	(notched-wing geometer)
Ennomos subsignaria (Hubner)	elm spanworm
Eotetranychus multidigituli (Ewing)	(a spider mite)
Epimecis hortaria (Fabricius)	(a looper)
Epinotia aceriella (Clemens)	maple trumpet skeletonizer
Epinotia meritana Heinrich	white fir needleminer
Epinotia nanana (Treitschke)	(a skeletonizer)
Epinotia subviridis Heinrich	(cypress leaftier)
Erannis tiliaria (Harris)	linden looper
Eriocampa ovata (Linnaeus)	(alder woolly sawfly)
Eriosoma lanigerum (Hausmann)	woolly apple aphid
Eriosoma rileyi Thomas	(woolly elm bark aphid)
Essigella gillettei Hottes	(an aphid)
Euceraphis betulae Koch	(an aphid)

Scientific name	Common name[1]
Eucosma bobana Kearfott	(pinyon cone borer)
Eucosma gloriola Heinrich	eastern pine shoot borer
Eucosma rescissoriana (Heinrich)	(lodgepole pine cone borer)
Eucosma siskiyouana (Kearfott)	(fir cone borer)
Eucosma sonomana Kearfott	western pineshoot borer
Eucosma tocullionana Heinrich	white pine cone borer
Eupithecia spermaphaga (Dyar)	fir cone looper
Euproctis chrysorrhoea (Linnaeus)	browntail moth
Eurytetranychus admes Prichard & Baker	(a spider mite)
Euzophera magnolialis Capps	(a pyralid moth)
Euzophera ostricolorella Hulst	(a pyralid moth)
Euzophera semifuneralis (Walker)	American plum borer
Exoteleia pinifoliella (Chambers)	pine needleminer
Fagiphagus imbricator (Fitch)	beech blight aphid
Fascista cercerisella (Chambers)	redbud leaffolder
Fenusa dohrnii (Tischbein)	European alder leafminer
Fenusa pusilla (Lepeletier)	birch leafminer
Ferrisia virgata Cockerell	striped mealybug
Formica exsectoides Forel	Allegheny mound ant
Galenara consimilis (Heinrich)	(New Mexico fir looper)
Gibbobruchus mimus (Say)	(a seed beetle)
Gilpinia hercyniae (Hartig)	European spruce sawfly
Gloveria arizonensis Packard	(a tent caterpillar)
Glycobius speciosus (Say)	sugar maple borer
Glyptoscelis aridis Van Dyke	(a leaf beetle)
Glyptoscelis vandykei Krauss	(a leaf beetle)
Gnathotrichus retusus (LeConte)	(an ambrosia beetle)
Gnathotrichus sulcatus (LeConte)	(an ambrosia beetle)
Goes pulcher (Haldeman)	(living-hickory borer)
Goes pulverulentus (Haldeman)	(living-beech borer)
Goes tesselatus (Haldeman)	oak sapling borer
Goes tigrinus (DeGeer)	white oak borer
Gonioctena americana (Schaeffer)	American aspen beetle
Gossyparia spuria (Modeer)	European elm scale
Gynaecia dirce (Linnaeus)	(a nymphalid butterfly)
Gypsonoma haimbachiana (Kearfott)	cottonwood twig borer
Halisidota argentata subalpina French	(a tiger moth)
Halisidota harrisii Walsh	sycamore tussock moth
Halisidota ingens Hy. Edwards	(a tiger moth)
Hemiberlesia rapax (Comstock)	greedy scale
Hemichroa crocea (Geoffroy)	striped alder sawfly
Hemicoelus spp.	powderpost beetle
Henricus fuscodorsanus (Kearfott)	(cone cochylid)
Heterarthrus nemoratus (Fallen)	(birch leaf-mining sawfly)
Heterocampa guttivitta (Walker)	saddled prominent
Heterocampa manteo (Doubleday)	variable oakleaf caterpillar
Heterotermes convexinotatus Snyder	(a termite)
Heterotermes tennis Hagan	(a termite)

Scientific name	Common name[1]
Historis odius (Fabricius)	(a nymphalid butterfly)
Homadaula anisocentra Meyrick	mimosa webworm
Hyalophora cecropia (Linnaeus)	cecropia moth
Hydria prunivorata (Ferguson)	(cherry scallop shell moth)
Hylecoetus lugubris Say	sapwood timberworm
Hylemya (Lasiomma) antracina (Czerny)	(spruce cone maggot)
Hylesinus oregonus (Blackman)	(Oregon ash bark beetle)
Hylobius pales (Herbst)	pales weevil
Hylobius radicis Buchanan	pine root collar weevil
Hylobius rhizophagus M., B., & W.	pine root tip weevil
Hylobius warreni Wood	(Warren's collar weevil)
Hylurgopinus rufipes (Eichhoff)	native elm bark beetle
Hyperaspis signata (Olivier)	(a ladybird beetle)
Hyphantria cunea (Drury)	fall webworm
Icerya purchasi Maskell	cottony cushion scale
Ichthyura inclusa (Hubner)	poplar tentmaker
Illinoia liriodendri Monell	tuliptree aphid
Ips calligraphus (Germar)	(sixspined ips)
Ips confusus (LeConte)	(piñon ips)
Ips emarginatus (LeConte)	(emarginate ips)
Ips grandicollis (Eichhoff)	(southern pine engraver)
Ips latidens (LeConte)	(a bark beetle)
Ips lecontei Swaine	(Arizona fivespined ips)
Ips mexicanus (Hopkins)	(Monterey pine ips)
Ips montanus (Eichhoff)	(an engraver beetle)
Ips paraconfusus Lanier	California fivespined ips
Ips pilifrons Swaine	(an engraver beetle)
Ips pini (Say)	pine engraver
Ips plastographus (LeConte)	(California fourspined ips)
Ips spinifer (Eichhoff)	(an engraver beetle)
Itame pustularia (Guenee)	(a spanworm)
Janus abbreviatus (Say)	willow shoot sawfly
Kaltenbachiella ulmifusa (Walsh & Riley)	(a gall aphid)
Kermes pubescens Bogue	(a scale insect)
Kleidocerys resedae germinatus (Say)	(a lygaeid bug)
Knulliana cincta (Drury)	banded hickory borer
Lambdina athasaria pellucidaria (Grote & Robinson)	(a geometrid)
Lambdina fiscellaria fiscellaria (Guenee)	hemlock looper
Lambdina fiscellaria lugubrosa (Hulst)	western hemlock looper
Lambdina fiscellaria somniaria (Hulst)	western oak looper
Lambdina pellucidaria (Grote & Robinson)	(a geometrid)
Laspeyresia bracteatana (Fernald)	fir seed moth
Laspeyresia caryana (Fitch)	hickory shuckworm
Laspeyresia injectiva (Heinrich)	(Jeffrey pine seedworm)
Laspeyresia piperana (Kearfott)	(ponderosa pine seedworm)
Laspeyresia populana Busck	(a bark moth)
Laspeyresia youngana (Kearfott)	spruce seed moth
Lecanium fletcheri Ckll.	(a scale insect)
Leperisinus aculeatus (Say)	(eastern ash bark beetle)
Lepidosaphes ulmi (Linnaeus)	oystershell scale
Leptocoris trivittatus (Say)	boxelder bug

Scientific name	Common name[1]
Leptoglossus corculus (Say)	(southern pine seed bug)
Leptoypha minor McAtee	(Arizona ash lace bug)
Leucoma salicis (Linnaeus)	satin moth
Lithocolletis salicifoliella Chambers	(a leafblotch miner)
Lithophane antennata (Walker)	green fruitworm
Longistigma caryae (Harris)	giant bark aphid
Lymantria dispar (Linnaeus)	gypsy moth
Macrohaltica ambiens (LeConte)	alder flea beetle
Magdalis gentilis LeConte	(a weevil)
Magicicada septendecim (Linnaeus)	periodical cicada
Malacosoma americanum (Fabricius)	eastern tent caterpillar
Malacosoma californicum (Packard)	western tent caterpillar
Malacosoma constrictum (Hy. Edwards)	Pacific tent caterpillar
Malacosoma disstria Hubner	forest tent caterpillar
Maladera castanea (Arrow)	Asiatic garden beetle
Marmara arbutiella Busck	(a twig and leaf miner)
Matsucoccus acalyptus Herbert	(piñon pine scale)
Matsucoccos bisetosus Morrison	(two seta pine scale)
Matsucoccus californicus Morrison	(California pine scale)
Matsucoccus fasciculensis Herbert	(fascicle pine scale)
Matsucoccus gallicola Morrison	(pine twig gall scale)
Matsucoccus monophyllae McKenzie	(a scale)
Matsucoccus paucicicatrices Morrison	(sugar pine scale)
Matsucoccus resinosae Bean & Godwin	red pine scale
Mayetiola carpophaga (Tripp)	(spruce seed midge)
Mayetiola thujae (Hedlin)	(a gall midge)
Megacyllene caryae (Gahan)	painted hickory borer
Magacyllene robiniae (Forster)	locust borer
Megastigmus atedius Walker	(a seed chalcid)
Megastigmus laricis Marcovitch	(a seed chalcid)
Megastigmus lasiocarpae Crosby	(a seed chalcid)
Megastigmus pinus Parfitt	(fir seed chalcid)
Megastigmus specularis Walley	(balsam fir seed chalcid)
Megastigmus spermotrophus Wachtl	(Douglas-fir seed chalcid)
Megastigmus tsugae Crosby	(a seed chalcid)
Malalgus confertus (LeConte)	(a false powderpost beetle)
Melanaspis obscura (Comstock)	obscure scale
Melanaspis tenebricosa (Comstock)	gloomy scale
Melanolophia imitata (Walker)	(greenstriped forest looper)
Melanophila californica Van Dyke	California flatheaded borer
Melanophila drummondi (Kirby)	flatheaded fir borer
Melanophila fulvoguttata (Harris)	hemlock borer
Melipotis indomita (Walker)	(a caterpillar)
Melissopus latiferreanus (Walsingham)	filbertworm
Mesa populifoliella (Townsend)	(a leafmining sawfly)
Mesolecanium nigrofasciatum (Pergande)	terrapin scale

Scientific name	Common name[1]
Mimosestes amicus (Horn)	(a seed beetle)
Monocesta coryli (Say)	larger elm leaf beetle
Monochamus spp.	(a wood borer)
Monoctenus melliceps (Cresson)	(a sawfly)
Mordvilkoja vagabunda (Walsh)	poplar vagabond aphid
Mycetococcus ehrhorni (Cockerell)	(Ehrhorn's oak scale)
Myrmelachista ramulorum Wheeler	(an ant)
Nasutitermes corniger Motschulsky	(a termite)
Nematocampa limbata (Haworth)	filament bearer
Nematus currani Ross	(a sawfly)
Nematus ventralis Say	willow sawfly
Neoclytus acuminatus (Fabricius)	redheaded ash borer
Neoclytus caprea (Say)	(banded ash borer)
Neodiprion abbotii (Leach)	(a sawfly)
Neodiprion approximatus Hopkins	(northern pine weevil)
Neodiprion burkei Middleton	lodgepole sawfly
Neodiprion compar (Leach)	(a sawfly)
Neodiprion dubiosus Schedl	brownheaded jack pine sawfly
Neodiprion edulicolus Ross	(piñon sawfly)
Neodiprion excitans Rohwer	blackheaded pine sawfly
Neodiprion lecontei (Fitch)	redheaded pine sawfly
Neodiprion nanulus nanulus Schedl	red pine sawfly
Neodiprion nigroscutum Middleton	(a sawfly)
Neodiprion pinetum (Norton)	white pine sawfly
Neodiprion pinusrigidae (Norton)	(a sawfly)
Neodiprion pratti banksianae Rohwer	jack pine sawfly
Neodiprion pratti paradoxicus Ross	(a sawfly)
Neodiprion pratti pratti (Dyar)	Virginia pine sawfly
Neodiprion sertifer (Geoffroy)	European pine sawfly
Neodiprion swainei Middleton	Swaine jack pine sawfly
Neodiprion taedae linearis Ross	loblolly pine sawfly
Neodiprion tsugae Middleton	hemlock sawfly
Neolecanium cornuparvum (Thro)	magnolia scale
Neophasia menapia (Felder & Felder)	pine butterfly
Nepytia canosaria (Walker)	false hemlock looper
Nepytia phantasmaria (Strecker)	phantom hemlock looper
Nerice bidentata Walker	(a notodontid moth)
Neuroterus saltatorius (Hy. Edwards)	(a jumping gall wasp)
Neurotoma fasciata (Norton)	(a web-spinning sawfly)
Norape ovina (Sepp)	(a flannel moth)
Nuculaspis californica (Coleman)	black pineleaf scale
Nygmia phaeorrhoea (Donov)	brown-tail moth
Nymphalis antiopa (Linnaeus)	mourningcloak butterfly
Oberea ferruginea Casey	willow-branch borer
Oberea schaumi LeConte	(a roundheaded borer)
Oberea tripunctata (Swederus)	dogwood twig borer
Obrussa ochrefasciella (Chambers)	hard maple budminer

Scientific name	Common name[1]
Odontopus calceatus (Say)	(a snout beetle)
Odontota dorsalis (Thunberg)	locust leafminer
Oecanthus fultoni T. J. Walker	snowy tree cricket
Oeme rigida (Say)	(a roundheaded borer)
Olesicampe benefactor Hinz	(an ichneumonid parasite)
Oligonychus ilicis (McGregor)	southern red mite
Oligonychus ununguis (Jacobi)	spruce spider mite
Oligotrophus betheli Felt	juniper tip midge
Oncideres cingulata (Say)	twig girdler
Oncideres pustulata LeConte	(huisache girdler)
Operophtera bruceata (Hulst)	Bruce spanworm
Orgyia leucostigma (J. E. Smith)	whitemarked tussock moth
Orgyia pseudotsugata (McDunnough)	Douglas-fir tussock moth
Orgyia vetusta (Boisduval)	western tussock moth
Otiorhynchus ovatus (Linnaeus)	strawberry root weevil
Otiorhynchus sulcatus (Fabricius)	black vine weevil
Pachylobius picivorus (Germar)	pitch-eating weevil
Pachypsylla celtidisgemma Riley	budgall psyllid
Pachypsylla celtidismamma (Riley)	(hackberry nipplegall maker)
Pachypsylla celtidisvesicula Riley	(blistergall psyllid)
Pachypsylla venusta (Osten Sacken)	(petiolegall psyllid)
Paleacrita vernata (Peck)	spring cankerworm
Pandemis cerasana (Hubner)	(a leafroller moth)
Pantographa limata Grote & Robinson	basswood leafroller
Pantomorus cervinus (Boheman)	Fuller rose beetle
Paraclemensia acerifoliella (Fitch)	maple leafcutter
Paradiplosis tumifex Gagne	(balsam gall midge)
Paranthrene dollii dollii (Newman)	(a clearwing moth)
Paranthrene simulans (Grote)	(clearwing borer)
Paranthrene tabaniformis (Rottenberg)	(a clearwing moth)
Parorgyia plagiata Walker	pine tussock moth
Parthenolecanium corni (Bouche)	European fruit lecanium
Parthenolecanium fletcheri (Cockerell)	Fletcher scale
Pentamerismus erythreus (Ewing)	(a false spider mite)
Periphyllus lyropictus (Kessler)	Norway maple aphid
Periphyllus negundinis (Thomas)	boxelder aphid
Periploca atrata Hodges	(a moth)
Pero behrensaria (Packard)	(a spanworm)
Petrova albicapitana arizonensis (Heinrich)	(piñon pitch nodule moth)
Petrova sabiniana (Kearfott)	(a pitch nodule moth)
Phenacoccus acericola King	(maple phenacoccus)
Phigalia titea Cram.	half wing geometer
Phloeosinus canadensis Swaine	(a bark beetle)
Phloeosinus cristatus (LeConte)	(cypress bark beetle)
Phloeosinus cupressi Hopkins	(a bark beetle)
Phloeosinus dentatus (Say)	(eastern juniper bark beetle)
Phloeosinus hoferi Blackman	(a bark beetle)
Phloeosinus scopulorum Swaine	(a bark beetle)
Phloeosinus sequoiae Hopkins	(redwood bark beetle)
Phloeosinus serratus (LeConte)	(a bark beetle)
Phloeosinus taxodii Blackman	(southern cypress beetle)
Phloeotribus liminaris (Harris)	peach bark beetle
Phoracantha semipunctata (Fabricius)	(a wood borer)
Phryganidia californica Packard	California oakworm
Phyllobius intrusus Kono	arborvitae weevil
Phyllobius oblongus (Linnaeus)	(European snout beetle)
Phyllocnistis magnoliella Fabricius	(a leafminer)
Phyllocnistis populiella Chambers	(aspen leafminer)
Phyllocolpa bozemani (Cooley)	(poplar leaffolding sawfly)
Phyllonorycter tremuloidiella Braun	(aspen blotch miner)
Phyllophaga forsteri Burmeister	(a scarab beetle)
Phylloxera caryaecaulis (Fitch)	(hickory gall aphid)
Phymatodes aeneus LeConte	(a roundheaded borer)
Phymatodes nitidus LeConte	(a roundheaded borer)
Phytobia pruinosa (Coquillett)	(a leafminer fly)
Phytobia pruni (Grossenbacher)	(a leafminer fly)
Phytobia setosa (Loew)	(a cambium miner)
Phytomyza ilicicola Loew	native holly leafminer
Pikonema alaskensis (Rohwer)	yellowheaded spruce sawfly
Pikonema dimmockii (Cresson)	greenheaded spruce sawfly
Pineus coloradensis (Gillette)	(a woolly aphid)
Pineus patchae Borner	(a gall)
Pineus pinifoliae (Fitch)	pine leaf adelgid
Pissodes approximatus Hopkins	northern pine weevil
Pissodes dubius Randall	(a snout beetle)
Pissodes radiatae Hopkins	Monterey pine ips
Pissodes strobi (Peck)	white pine weevil
Pissodes terminalis Hopping	lodgepole terminal weevil
Pityogenes carinulatus LeConte	(a bark beetle)
Pityogenes fossifrons (LeConte)	(a bark beetle)
Pityophthorus lautus (Eichhoff)	(a bark beetle)
Pityophthorus liquidambarus Blackman	(a bark beetle)
Pityophthorus nitidus Swaine	(a bark beetle)
Pityophthorus toralis (Wood)	(a bark beetle)
Placosternus crinicornis (Chevrolat)	kiawe roundheaded borer
Plagiodera versicolora (Laicharting)	imported willow leaf beetle
Plagithmysus bilineatus Sharp	(a roundheaded borer)
Plagodis serinaria Herrich-Schaeffer	(a spanworm)
Platypus compositus (Say)	(a pinhole borer)
Platypus quadridentatus (Olivier)	(a pinhole borer)
Plectrodera scalator (Fabricius)	cottonwood borer
Pleuroptya salicalis (Guenee)	(a pyralid moth)
Podosesia syringae (Harris)	ash borer, lilac borer
Poecilonota cyanipes (Say)	(a flatheaded borer)
Poecilonota montana Chamberlin	(a flatheaded borer)
Polycanon stouti (LeConte)	(a false powderpost beetle)
Polydesma umbricola Boisduval	monkeypod moth
Polygraphus rufipennis (Kirby)	(foureyed spruce beetle)
Popillia japonica Newman	Japanese beetle

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Scientific name	Common name[1]
Prionoxystus macmurtrei (Guerin)	little carpenterworm
Prionoxystus robiniae (Peck)	carpenterworm
Prionus imbricornis (Linnaeus)	tilehorned prionus
Prionus laticollis (Drury)	broadnecked root borer
Pristiphora erichsonii (Hartig)	larch sawfly
Pristocauthophilus pacificus Thomas	mushroom camel cricket
Probole amicaria (Herrich-Schaeffer)	(a geometrid moth)
Prociphilus americanus (Walker)	(an aphid)
Prociphilus tesselatus (Fitch)	(woolly alder aphid)
Prodiplosis morrisi Gagne	(a poplar gall midge)
Profenusa lucifex (Ross)	(a leaf miner)
Profenusa thomsoni (Konow)	(a birch leaf mining sawfly)
Prosapia bicincta (Say)	twolined spittlebug
Protalebra tabebuiae Dozier	(a leafhopper)
Proteoteras willingana Kearfott	(boxelder twig borer)
Pseudococcus comstocki (Kuwana)	comstock mealybug
Pseudococcus maritimus Ehrhorn	grape mealybug
Pseudohylesinus dispar Blackman	(a bark beetle)
Pseudohylesinus granulatus (LeConte)	(fir root bark beetle)
Pseudohylesinus nobilis Swaine	(noble fir bark beetle)
Pseudohylesinus sericeus (Mannerheim)	(silver fir beetle)
Psylla uncatoides Ferris & Klyver	acacia psyllid
Ptilinus basalis LeConte	(a powderpost beetle)
Ptosima gibbicollis (Say)	(a flatheaded borer)
Pulvinaria acericola (Walsh & Riley)	(cottony maple leaf scale)
Pulvinaria innumerabilis (Rathvon)	cottony maple scale
Puto cupressi (Coleman)	(fir mealybug)
Puto pricei McKenzie	(price mealybug)
Pyrrhalta cavicollis (LeConte)	cherry leaf beetle
Pyrrhalta decora (Say)	(a leaf beetle)
Pyrrhalta decora decora (Say)	gray willow leaf beetle
Pyrrhalta luteola (Muller)	elm leaf beetle
Pyrrhalta punctipennis (Mannerheim)	(a leaf beetle)
Quadraspidiotus juglansregiae (Comstock)	walnut scale
Quadraspidiotus perniciosus (Comstock)	San Jose scale
Quernaspis quercus (Comstock)	(oak scale)
Resseliella clavula Beutenmuller	(a gall midge)
Rhabdophaga swainei Felt	spruce bud midge
Rheumaptera hastata (Linnaeus)	spearmarked black moth
Rhyacionia adana Heinrich	(a pine shoot moth)
Rhyacionia buoliana (Schiffermuller)	European pine shoot moth
Rhyacionia frustrana (Comstock)	Nantucket pine tip moth
Rhyacionia rigidana (Fernald)	pitch pine tip moth
Rhyacionia zozana Kearfott	(ponderosa pine tip moth)
Sabulodes aegrotata (Guenee)	omnivorous looper
Samia cynthia (Drury)	cynthia moth
Sannina uroceriformis Walker	persimmon borer
Saperda calcarata Say	poplar borer
Saperda discoidea Fabricius	(a roundheaded borer)
Saperda inornata Say	(poplar gall borer)
Saperda moesta LeConte	(a roundheaded borer)
Saperda tridentata Olivier	elm borer
Saperda vestita Say	linden borer
Scaphoideus luteolus Van Duzee	whitebanded elm leafhopper
Schizura concinna (J. E. Smith)	redhumped caterpillar
Sciaphila duplex (Walsingham)	(aspen leaftier)
Sciaphilus asperatus (Bonsdorff)	(a weevil)
Scobicia bidentata (Horn)	(a false powderpost beetle)
Scolytus laricis Blackman	(larch engraver)
Scolytus mali (Bechstein)	larger shothole borer
Scolytus multistriatus (Marsham)	smaller European elm bark beetle
Scolytus muticus Say	hackberry engraver
Scolytus quadrispinosus Say	hickory bark beetle
Scolytus ventralis LeConte	fir engraver
Scotorythra paludicola (Butler)	koa moth
Seinarctica echo (J. E. Smith)	(a webworm)
Semanotus amethystinus (LeConte)	(amethyst cedar borer)
Semanotus juniperi (Fisher)	(a roundheaded borer)
Semanotus ligneus (Fabricius)	cedartree borer
Semiothisa sexmaculata incolorata (Dyar)	(larch looper)
Semudobia betulae (Winnertz)	(a birch midge)
Smodicum cucujiforme (Say)	(flat powderpost beetle)
Sparganothis acerivorana MacKay	(a leafroller)
Sparganothis dilutocostana (Walsingham)	(a leafroller)
Sparganothis reticulatana (Clemens)	(a leafroller moth)
Sphinx chersis (Hubner)	great ash sphinx
Sphinx kalmiae J. E. Smith	(a sphinx moth)
Sphinx sequoiae Boisduval	(a sphinx moth)
Stator limbatus (Horn)	(a seed beetle)
Stenodontes dasytomus (Say)	(hardwood stump borer)
Steremnius carinatus (Boheman)	(a weevil)
Stictocephala militaris Gibson & Wells	(a treehopper)
Stilpnotia salicis Linnaeus	satin moth
Styloxus bicolor (Champlain & Knull)	(juniper twig pruner)
Symmerista albifrons (J. E. Smith)	(an oakworm)
Symmerista canicosta Franclemont (=*albicosta* Hbn.)	(redhumped oakworm)
Synanthedon acerni (Clemens)	maple callus borer
Synanthedon pictipes (Grote & Robinson)	lesser peachtree borer
Synanthedon scitula (Harris)	dogwood borer
Synanthedon sequoiae (Hy. Edwards)	(sequoia pitch moth)
Synaphaeta guexi (LeConte)	(a roundheaded borer)
Syntexis libocedrii Rohwer	incense-cedar wasp
Systena marginalis (Illiger)	(a leaf beetle)

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Taniva abolineana (Kearfott)	(spruce needle miner)
Tegolophus spongiosus Styer	(a mite)
Tethida barda (Say)	blackheaded ash sawfly
Tetralopha asperatella (Clemens)	(a webworm)
Tetralopha robustella Zeller	pine webworm
Tetraneura ulmi (Linnaeus)	(a gall aphid)
Tetranychus canadensis (McGregor)	fourspotted spider mite
Tetranychus magnoliae Boud.	spider mite
Tetranychus urticae Koch	twospotted spider mite
Tetropium abietis Fall	roundheaded fir borer
Tetropium velutinum LeConte	(western larch borer)
Tetyra bipunctata (Herrich-Schaeffer)	shieldbacked pine seedbug
Thrips madronii Moulton	(a narrowwinged thrips)
Thyridopteryx ephemeraeformis (Haworth)	bagworm
Thysanoes fimbricornis LeConte	(a bark beetle)
Tinocallis ulmifolii (Monell)	elm leaf aphid
Tomostethus multicinctus (Rohwer)	brownheaded ash sawfly
Toumeyella liriodendri (Gmelin)	tuliptree scale
Toumeyella parvicornis (Cockerell)	pine tortoise scale
Trachykele blondeli Marseul	(western cedar borer)
Trachykele opulenta Fall	(a flatheaded borer)
Trioza magnoliae (Ashmead)	(a psyllid)
Trisetacus floridanus Keifer	(a mite)
Trisetacus neoquadrisetus Smith	(a mite)
Trisetacus quadrisetus (Thomas)	(juniper berry mite)
Tropidosteptes pacificus (Van Duzee)	(a plant bug)
Trypodendron betulae Swaine	(an ambrosia beetle)
Trypodendron lineatum (Olivier)	striped ambrosia beetle
Trypodendron retusum (LeConte)	(an ambrosia beetle)
Tuberculatus columbiae Richards	(an aphid)
Tylonotus bimaculatus Haldeman	(ash and privet borer)
Vaga blackburni (Tuely)	Blackburn butterfly
Valentinia glandulella (Riley)	(acorn moth)
Vasates aceris-crummena Riley	(a bladdergall mite)
Vasates quadripedes Shimer	maple bladdergall mite
Vespamima sequoiae (Hy. Edwards)	(sequoia pitch moth)
Walshomyia insignis Felt	(a gall midge)
Walshomyia sabinae (Patterson)	(a gall midge)
Xestobium spp.	powderpost beetle
Xiphydria abdominalis Say	(a horntail)
Xiphydria maculata Say	(a horntail)
Xyleborinus saxesensi (Ratzeburg)	(an ambrosia beetle)
Xyleborus affinis Eichhoff	(an ambrosia beetle)
Xyleborus ferrugineus (Fabricius)	(an ambrosia beetle)
Xyleborus simillimus Perkins	(an ambrosia beetle)
Xylobiops basilaris (Say)	(a false powderpost beetle)
Xylococculus betulae (Pergande)	(birch margarodid)
Xylosandrus compactus (Eichhoff)	black twig borer
Xylosandrus germanus (Blandford)	(an ambrosia beetle)
Xyloterinus politus (Say)	(an ambrosia beetle)
Xylotrechus aceris Fisher	gallmaking maple borer
Xylotrechus obliteratus LeConte	(poplar-butt borer)
Xystrocera globosa (Olivier)	monkeypod roundheaded borer
Zadiprion rohweri (Middleton)	(a sawfly)
Zeiraphera improbana (Walker)	(larch bud moth)
Zelleria haimbachi Busck	pine needle sheathminer
Zeugophora scutellaris Suffrian	(a leaf beetle)
Zeuzera pyrina (Linnaeus)	leopard moth

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[1] Names without parentheses are approved by the Entomological Society of America.

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Checklist of Organisms Causing Tree Diseases

Scientific binomial	Synonym	Common name or symptom
Acremonium diospyri (Crand.) W. Gams	*Cephalosporium diospyri* Crand.	persimmon wilt
Actinopelte dryina (Sacc.) Hoehn.		Actinopelte leaf spot
Aecidium aesculi Ell. et Kellelm.		leaf spot
Agrobacterium tumefaciens (E. F. Smith et Town.) Conn.		crown gall
Alternaria tenuis Nees		Alternaria leaf and stem blight
Alerodiscus amorphus (Pers.: Fr.) Rab.		canker
Amphichaeta grevilleae Loos		silk-oak leaf spot
Anthostoma oreodaphnes		foliage discoloration
Apiosporium piniphilum Fckl.		sooty mold
Apiosporina morbosa (Schw.) von Arx	*Dibotryon morbosum* Th. et Syd.	black knot
Arceuthobium abietinum Engelm. ex Munz		fir dwarf mistletoe
Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. et Wiens		red fir dwarf mistletoe
Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. et Wiens		white fir dwarf mistletoe
Arceuthobium americanum Nutt. ex Engelm.		lodgepole pine dwarf mistletoe
Arceuthobium californicum Hawksw. et Wiens		sugar pine dwarf mistletoe
Arceuthobium campylopodium Engelm.		western dwarf mistletoe
Arceuthobium cyanocarpum Coulter et Nelson		limber pine dwarf mistletoe
Arceuthobium divaricatum Engelm.		pinyon dwarf mistletoe
Arceuthobium douglasii Engelm.		Douglas-fir dwarf mistletoe
Arceuthobium laricis (Piper) St. Johns		larch dwarf mistletoe
Arceuthobium microcarpum (Engelm.) Hawkins et Wiens		western spruce dwarf mistletoe
Arceuthobium occidentale Engelm.		digger pine dwarf mistletoe
Arceuthobium pusillum Pk.		eastern dwarf mistletoe
Arceuthobium tsugense (Rosend.) G. N. Jones		hemlock dwarf mistletoe
Arceuthobium vaginatum (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. et Wiens		southwestern dwarf mistletoe
Arceuthobium vaginatum (Willd.) Presl subsp. *vaginatum*		southwestern dwarf mistletoe
Armillaria mellea (Vahl.: Fr.) Kumm.	*Armillariella mellea* (Vahl.: Fr.) Karst.	shoestring root rot
Armillaria ostoyae (Romagn.) Herink		root disease
Ascochyta cornicola Sacc.		Ascochyta leaf blight
Astraeus pteridis (Shear) Zeller		earth star
Atropellis pinicola Zell. et Good.		Atropellis canker
Atropellis piniphila (Weir) Lohm. et Cash		branch canker
Atropellis tingens Lohm. et Cash		stem canker
Aureobasidium pullulans (de B.) Arn.	*Pullularia pullulans* (de B.) Berkh.	hemlock seed mold
Bifusella linearis (Pk.) Hoehn.		needle cast
Bifusella saccata (Darker) Darker		needle cast
Boletellus zelleri (Murr.) Sing.		mycorrhizal symbiont
Botryodiplodia theobromae Pat.		Botryodiplodia canker
Botryosphaeria dothidea (Moug.: Fr.) Ces. et deNot		madrone canker
Botryosphaeria ribis (Tode: Fr.) Gross. et Dug.		canker & trunk lesion
Botrytis cinerea Pers.: Fr.		Botrytis petal blight
Calonectria crotalariae (Loos) Bell et Sobers		koa crown rot
Calonectria thea Loos		koa shoot blight
Capnodium pini Berk. et Curt.		sooty mold
Cenangium furruginosum Fr.		Cenangium limb canker
Cenococcum graniforme (Sow.) Ferd. et Winge		mycorrhizal symbiont
Cephalosporium pallidum Verrall		wood stain fungus
Ceratocystis ambrosia Bak.		Ceratocystis canker
Ceratocystis cana (Muench) C. Mor.		Ceratocystis canker

Scientific binomial	Synonym	Common name or symptom
Ceratocystis coerulescens (Muench) Bak.		sapstreak
Ceratocystis crassivaginata H. D. Griffin		Ceratocystis canker
Ceratocystis fagacearum (Bretz) Hunt		oak wilt
Ceratocystis fimbriata Ell. et Halst.		Ceratocystis canker
Ceratocystis moniliformis (Hedg.) C. Mor.		Ceratocystis canker
Ceratocystis piceae (Muench) Bak.		Ceratocystis canker
Ceratocystis pluriannulata (Hedg.) C. Mor.		sapwood stain
Ceratocystis serpens (Goid.) C. Mor.		Ceratocystis canker
Ceratocystis tremul-aurea Davidson et Hinds		Ceratocystis canker
Ceratocystis ulmi (Buism.) C. Mor.		Dutch elm disease
Cercospora aesculina Ell. et Kellerm.		leaf spot
Cercospora circumcissa Sacc.		leaf spot
Cercospora cornicola Tr. et Earle		dogwood leaf spot
Cercospora halstedii Ell. et Ev.		leaf blotch
Cercospora maclurae Ell. et Ev.		leaf spot
Cercospora microsora Sacc.		basswood leaf spot
Cercospora pulvinula Cke. et Ell.		holly leaf spot
Cercospora sequoiae Ell. et Ev.		foliage blight
Cercospora spegazzinii Sacc.		leaf spot
Cercosporella celtidis (Ell. et Kellerm.) J. J. Davis		leaf spot
Cerotelium fici (Butl.) Arth.		leaf spot
Ceuthocarpum conflictum (Cke.) Berl.		leaf spot
Chlorogenus robiniae Holmes		witches' broom virus
Chrysomyxa arctostaphyli Diet.		yellow witches' broom
Chrysomyxa chiogenis Arth.		needle rust
Chrysomyxa empetri Pers.		needle rust
Chrysomyxa ilicina (Arth.) Arth.		holly rust
Chrysomyxa ledi de B.		needle rust
Chrysomyxa ledicola Lagh.		spruce needle rust
Chrysomyxa pirolata Wint.		spruce cone rust
Chrysomyxa weirii Jacks.		needle rust
Chrysomyxa woroninii Tranz.		bud rust
Ciboria acerina Whetz. et Buchew.		maple flower blight
Cladosporium effusum (Wint.) Dem.		pecan scab
Cladosporium humile J. J. Davis		leaf spot
Climacocystis borealis (Fr.) Kotl. et Pouz.	*Polyporus borealis* Fr.	heart rot
Climacodon septentrionalis (Fr.) Karst.	*Hydnum septentrionalis* Fr.	white heart rot
Clitocybe tabescens (Scop.: Fr.) Bres.	*Armillaria tabescens* (Scop.: Fr.) Bres.	mushroom root rot
Coccomyces hiemalis Higg.		cherry leaf spot
Coccomyces lutescens Higg.		cherry leaf spot
Coleosporium asterum (Diet.) Syd.	*Coleosporium solidaginis* (Schw.) Thum.	needle rust
Coleosporium campanulae (Pers.) Lev.		needle rust
Coleosporium crowellii Cumm.		needle rust
Coleosporium helianthi (Schw.) Arth.		needle rust
Coleosporium jonesii (Pk.) Arth.		needle rust
Coleosporium madiae Cke.		tarweed rust
Colletotrichum gloeosporioides Penz.		leaf spot
Collybia velutipes (Fr.) Kumm.	*Flammulina velutipes* (Fr.) Karst.	heart rot
Coniophora corrugis Burt		sapwood and heartwood rot
Coniophora olivacea (Fr.) Karst.	*Coniophorella olivacea* (Fr.) Karst.	root and butt rot
Coniophora puteana (Schum.: Fr.) Karst	*Coniophorella puteana* Schum.: Fr.	root and butt rot
Conophilis americana (L.) Wallr.	*Coniophora cerebella* (Pers.) Pers.	root rot squaw root
Conothyrium truncisedum Vestergr.		leaf spot
Coprinus atramentarius (Bull: Fr.) Fr.		root rot
Corticium expallense Bres.	*Phlebia expallense* (Bres.) Parm.	decay fungus
Corticium salmonicolor Berk. et Br.	*Phanerochaete salmonicolor* (Berk. et Br.) Jülich	dieback

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Corynebacterium ilicis Mandel, Guba et Litsky		leaf and twig blight
Coryneum carpophyllum (Lev.) Jauch.		leaf spot
Criconemoides quadricornis (Kirhanova) Raski		ring nematode
Cristulariella depraedens (Cke.) Hoehn.		leaf spot
Cristulariella pyramidalis Wat. et Marsh.		target leaf spot
Cronartium coleosporioides (Diet. et Holw.) Arth.		pine stem rust
Cronartium comandrae Pk.		Comandra blister rust
Cronartium comptoniae Arth.		sweetfern rust
Cronartium occidentale Hedgc., Bethel et Hunt		pinyon blister rust
Cronartium quercuum (Berk.) Miy. ex Shirai f. sp. *fusiforme* Burds. et Snow	*Cronartium fusiforme* Hedgc. et Hunt	fusiform rust
Cronartium quercuum (Berk.) Miy. ex Shirai	*Cronartium quercuum* (Berk.) Miy. ex Shirai f. sp. *quercuum*	eastern gall rust
Cronartium ribicola Fischer		white pine blister rust
Cryphonectria cubensis (Bruner) Hodges	*Diaporthe cubensis* Bruner	eucalyptus canker
Cryphonectria parasitica (Murr.) Barr	*Endothia parasitica* (Murr.) P. J. et H. W. And.	chestnut blight
Cryptosphaeria populina (Pers.: Fr.) Sacc.		Cryptosphaeria canker
Cryptosporium pinicola Lind.		stem and branch canker
Cryptostroma corticale (Ell. et Ev.) Greg. et Wall.		sooty bark
Cucurbitaria staphula Dearn. ex Arnold et Russell		rough, corky bark
Cylindrocarpon cylindroides Wollenw.		stem and branch canker
Cylindrocladium floridanum Sob. et Seymour		Cylindrocladium root rot
Cylindrocladium scoparium Morg.		Cylindrocladium root rot
Cylindrosporium californicum Earle		leaf spot
Cylindrosporium defoliatum Heald et Wolf		leaf spot
Cylindrosporium juglandis Wolf		leaf spot
Cylindrosporium fraxini (Ell. et Kellerm.) Ell. et Ev.		leaf spot
Cytophoma pruinosa (Fr.) Hoehn.		ash canker
Cytospora abietis Sacc.		stem and branch canker
Cytospora ambiens Sacc.		twig fungus
Cytospora chrysosperma Pers.: Fr.		Cytospora canker
Cytospora leucostoma Sacc.		canker
Cytospora tumulosa Ell. et Ev.		branch saprophyte
Cytosporina ludibunda Sacc.		elm wilt and dieback
Daedalea ambigua Berk.	*Daedalea elegans* Spring.: Fr.	heart rot
Daedalea juniperina Murr.	*Antrodia juniperina* (Man.) Niem et Ryv.	heart rot
Daedalea quercina L.: Fr.		heart rot
Daedalea unicolor (Bull.: Fr.) Murr.	*Cerrena unicolor* (Bull.: Fr.) Murr.	canker rot
Dasyscypha agassizii (Berk. et Curt.) Sacc.		saprophyte on bark
Dasyscypha arida (Phill.) Sacc.		saprophyte on bark
Dasyscypha pini Hahn et Ayers		saprophyte on bark
Dasyscypha willkommii (Hart.) Rehm		European larch canker
Davisomycella ampla (Dav.) Darke		needle cast
Diaporthe alleghaniensis R. H. Arnold		black sunken canker and shoot blight
Dichomitus squalens (Karst.) Reid	*Polyporus anceps* Pk.	western root rot
Didymascella tetramicrospora Pant. et Darker		leaf blight
Didymascella thujina (Durand) Maine		seedling and foliage blight
Didymosphaeria oregonensis Good.		alder stem and branch canker
Dimerium juniperi Dearn.		smudge mold
Dimerosporium tsugae Dearn.		sooty mold of hemlock
Diplodia longispora Cke. et Ell.		twig blight

Scientific binomial	Synonym	Common name or symptom
Diplodia pinea (Desm.) Kickx	*Sphaeropsis sapinea* (Fr.: Fr.) Dyko et Sutton	Diplodia tip blight
Diplodia taxi (Sowerby) deNot		stem canker
Diplodia tumefaciens (Shear) Zalasky		rough, corky bark
Discula quercina (Westd.) v. Arx		anthracnose
Dothichiza populea Sacc. et Briard.		Dothichiza canker
Dothiorella quercina (Cke. et Ell.) Sacc.		Dothiorella canker
Dothiorella ulmi Verr. et May		elm dieback
Dothistroma pini Hulb.		Dothistroma needle blight
Echinodontium taxodii (Lentz et McKay) Gross	*Stereum taxodii* Lentz et McKay	pecky cypress pocket rot
Echinodontium tinctorium (Ell. et Ev.) Ell. et Ev.		Indian paint fungus
Elaphomyces granulatus Fr.		mycorrhizal symbiont
Elsinoe corni Jenk. et Bitan.		dogwood leaf spot
Elsinoe quercus-falcatae J. Mill.		spot anthracnose
Elsinoe randii Jenk. et Bitan.		pecan spot anthracnose
Elytroderma deformans (Weir) Darker		needle cast
Encoeliopsis laricina (Ettl.) Groves		larch shoot blight
Endocronartium harknessii (J. P. Moore) Y. Hirat	*Peridermium harknessii* J. P. Moore	western gall rust
Endoraceium acaciae C.S. Hodges et D. E. Gardner		rust fungus
Endoraceium hawaiiense C.S. Hodges et D. E. Gardner		rust fungus
Endothia gyrosa (Schw.: Fr.) Fr.		pin oak blight
Endothia havaensis Bruner	*Cryphonectria havanensis* (Bruner) Barr	canker disease
Epifagus virginiana (L.) Bart.		beech drops
Erwinia nimipressuralis Cart.		elm wetwood
Erysiphe cichoracearum DC.		powdery mildew
Eutypella parasitica Davidson et Lorenz		Eutypella canker
Fabrella tsugae (Farl.) Kirschst.	*Didymascella tsugae* (Farl.) Maire	hemlock needle blight
Fomes fomentarius (L.: Fr.) Kickx		trunk rot
Fomes geotropus Cke.		heart rot
Fomes nobilissimus (Cke.) Lowe		trunk rot
Fomes sclerodermeus (Lev.) Cke.	*Fomes marmoratus* (Berk. et Curt.) Cke.	white heart rot
Fomes subroseus Weir	*Fomitopsis cajanderi* (Karst.) Kotl. et Pous.; *Fomes cajanderi* Karst.	heart rot
Fomitopsis cajanderi (Karst.) Kotl. et Pouz.	*Fomes subroseus* Weir; *Fomes cajanderi* Karst.	heart rot
Fomitopsis fraxineus (Bull.: Fr.)	*Fomes fraxineus* (Bull.: Fr.) Cke.	wood rot
Fomitopsis officinalis (Vill.: Fr.) Bond. et Singer	*Fomes officinalis* (Vill.: Fr.) Faull	quinine fungus
Fomitopsis pinicola (Schwartz: Fr.) Karst.	*Fomes pinicola* (Schwartz: Fr.) Cke.	red belt fungus
Fomitopsis roseus (Alb. et Schw.: Fr.) Karst.	*Fomes roseus* (Alb. et Schw.: Fr.) Karst.	heart rot
Fomitopsis scutellata (Schw.) Bond. et Sing.	*Fomes scutellatus* (Schw.) Cke	wood rot
Fumago vagans Fr.		black mold
Fusarium oxysporum (Schl.) emend. Snyd. et Hans.		pecan feeder root necrosis
Fusarium reticulatum Mont. var. *negundinis* (Sherb.) Wr.	*Fusarium roseum* (Lk.) emend. Snyd. et Hans.	red stain of boxelder
Fusarium solani (Mart.) App. et Wr. emend. Snyd. et Hans.		pecan feeder root necrosis
Fusicoccum aesculi Corda in Sturm		madrone canker
Ganoderma applanatum (Pers.: Wallr.) Pat.	*Fomes applanatus* (Pers.: Wallr.) Gill	artist's conk
Ganoderma curtisii (Berk.) Murr.	*Polyporus curtisii* Berk.	root rot
Ganoderma lucidum (Leys. ex Fr.) Karst.		varnish or lacquer conk
Ganoderma tsugae Murr.	*Polyporus tsugae* (Murr.) Overh.	red varnish-top fungus
Gloeocystidiellum citrinum (Pers.) Donk	*Corticium radiosum* (Fr.: Pers.) Fr.	root and butt rot
Gloeocystidiellum radiosum		root and butt rot
Gloeosporium apocryptum Ell. et Ev.		anthracnose
Gloeosporium aridum Ell. et Holway		ash anthracnose

Scientific binomial	Synonym	Common name or symptom
Gloeosporium betularum Ell. et Mart.		anthracnose leaf blight
Gloeosporium saccharinum Ell. et Ev.		anthracnose
Gloeosporium ulmicolum Miles		leaf spot and twig blight
Glomus fasciculatus (Thaxter) Gerd. et Trappe		endomycorrhizal associate
Glomus mosseae (Nicol. et Gerd.) Gerd. et Trappe		endomycorrhizal associate
Gnomonia caryae Wolf		anthracnose
Gnomonia caryae var. *pecanae* Cole		pecan liver spot
Gnomonia leptostyla (Fr.) Ces. et deNot.		walnut anthracnose
Gnomonia nerviseda Cole		pecan vein spot
Gnomonia quercina Kleb.		oak anthracnose
Gnomonia satacea (Pers.: Fr.) Ces. et deNot.		canker, shoot blight, leaf spot
Gnomonia tiliae Kleb.		basswood anthracnose
Gnomonia ulmea (Schw.: Fr.) Thuem.		black spot of elm
Gnomonia veneta (Sacc. et Speg.) Kleb.	*Gnomonia paltani* Edg.	oak anthracnose
Gomphidius ochraceus Kauffm.		mycorrhizal symbiont
Gomphidius rutilus (Schael.: Fr.) Lund. & Nannf.		mycorrhizal symbiont
Gomphidius superiorensis Kauf. et Smith		mycorrhizal symbiont
Gomphidius vinicolor Pk.		mycorrhizal symbiont
Gremmeniella abietina (Lagerb.) Morelet	*Scleroderris lagerbergii* Grem.	Scleroderris canker
Guignardia aesculi (Pk.) Stew.		leaf blotch
Gymnopilus spectabilis (Fr.) Singer	*Pholiota spectabilis* (Fr.) Kumm.	trunk rot
Gymnosporangium bethelii Kern		juniper twig knot rust
Gymnosporangium biseptatum Ell.		stem and branch gall rust
Gymnosporangium clavipes (Cke. et Pk.) Cke. et Pk.		gall rust
Gymnosporangium effusum Kern		gall rust
Gymnosporangium ellisii (Berk.) Farlow		witches' broom rust
Gymnosporangium globosum Farlow		juniper branch gall rust
Gymnosporangium inconspicuum Kern		juniper witches' broom rust
Gymnosporangium juniperi-virginianae Schw.		cedar applerust
Gymnosporangium kernianum Bethel		brown rust
Gymnosporangium libocedri (P. Henn.) Kern		witches' broom rust
Gymnosporangium nelsonii Arth.		juniper stem gall rust
Gymnosporangium nidus-avis Thaxt.		juniper witches' broom rust
Haematostereum sanguinolentum (Alb. et Schw.: Fr.) Pouz.	*Stereum sanguinolentum* (Alb. et Schw.: Fr.) Fr.	red heart trunk rot
Helicobasidium purpureum (Tul.) Pat.		violet root rot
Hendersonula toruloidea Natt.		branch wilt and canker
Hericium coralloides (Scop.: Fr.) S. F. Gray	*Hydnum coralloides* Scop.: Fr.	trunk rot
Hericium erinaceum (Bull.: Fr.) Pers.	*Hydnum erinaceus* Bull.: Fr.	magnolia leaf spot
Herpotrichia nigra Hartig	*Herpotrichia juniperi* (Duby) Petrak	brown felt mold
Heterobasidion annosum (Fr.) Bref.	*Fomes annosus* (Fr.) Cke.	annosus root rot
Hirschioporus abietinus (Dicks.: Fr.) Donk	*Polyporus abietinus* Dicks.: Fr.	wood rot
Hydnum erinaceus Bull.: Fr.	*Hericium erinaceum* (Bull.: Fr.) Pers.	hedgehog fungus
Hymenochaete agglutinans Ell.		gluing fungus
Hypoderma hedgcokii Dearn.	*Ploioderma hedgcokii* (Dearn.) Darker	needle cast
Hypoderma lethale Dearn.	*Ploioderma lethale* (Dearn.) Darker	needle cast
Hypodermella laricis Tub.		larch needlecast
Hypoxylon mammatum (Wahl.) J. Miller	*Hypoxylon pruinatum* (Klot.) Cke.; *H. blakei* Berk. et Curt.	Hypoxylon canker
Hysterographium fraxini (Pers.: Fr.) deNot.		twig saprophyte
Inonotus andersonii (Ell. et Overh.) Cérny	*Poria andersonii* (Ell. et Ev.) Cérny	white pocket rot
Inonotus dryadeus (Pers.: Fr.) Murr.	*Polyporus dryadeus* Pers.: Fr.	white root rot
Inonotus dryophilus (Berk.) Murr.	*Polyporus dryophilus* Berk.	white pocket rot
Inonotus glomeratus (Pk.) Murr.	*Polyporus glomeratus* Pk.	wood rot

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Inonotus obliquus (Pers.: Fr.) Pilat	*Poria obliqua* (Pers.: Fr.) Karst.	heart rot
Inonotus rheades	*(Peniophora polygonia, americanum, rufa)*	trunk rot
Inonotus tomentosus (Fr.) Gilbertson	*Polyporus tomentosus* Fr.	heart rot
Kabatiella phoradendri Darker f. sp. *umbellulariae* Harv.		leaf spot
Keithia chamaecyparissi Adams	*Didymascella chamaecyparissi* (Adams) Maire	tip blight
Lachnellula occidentalis (Hahn et Ayers) Dharne		stem canker
Lachnellula suecica (de Bary ex Fuckel) Nannf.		stem canker
Laetiporus sulphureus (Bull.: Fr.) Bond et Singer	*Polyporus sulphureus* Bull.: Fr.	sulphur fungus
Lecanosticta acicola Theum. et Syd.		brown spot
Lentinus tigrinus Fr.		heart rot
Leuocytospora kunzei (Sacc.) Z. Urba	*(Cytospora kunzei* Sacc.)	branch canker
Linospora gleditsiae J. Miller et Wolf		tarry leaf spot
Lirula abietis-concoloris (Mayr ex Dearn.) Darker		needle cast
Lirula macrospora (Hartig) Darker	*Lophodermium filiforme* Darker	needle cast
Lirula punctata (Darker) Darker		needle cast
Lophodermella arcuata (Darker) Darker		needle cast
Lophodermella concolor (Darker) Darker		needle cast
Lophodermium autumnale Darker		needle cast
Lophodermium juniperinum (Fr.) deNot.		foliage necrosis
Lophodermium laricinum Duby		needle cast
Lophodermium nitens Darker		needle cast
Lophodermium piceae (Fckl.) Hoehn.		needle cast
Lophodermium pinastri (Schrad.) Chev.		needle cast
Lophodermium seditiosum Minter, Staley, et Millar		needle cast
Lophodermium uncinatum Darker		needle cast
Lophophacidium hyperboreum Lagerb.		snow blight
Macrophoma taxi Berl. et Vogl.		yellow needle blight
Macrophomina phaseoli (Maub.) Ashby		charcoal root rot
Marssonina brunnea (Ell. et Ev.) Sacc.		Marssonina leaf spot
Marssonina fraxini Niessl		leaf spot
Marssonina populi (Lib.) Magn.		leaf spot, shoot blight
Melampsora abietis-canadensis (Farlow) Ludw.		hemlock needle rust
Melampsora farlowii (Arth.) Davis		hemlock cone and shoot rust
Melampsora medusae Theum.		Melampsora leaf rust
Melampsorella caryophyllacearum Schroet.		fir broom rust
Melanconis juglandis (Ell. et Ev.) Graves		twig and branch dieback
Meliola koae Stevens		koa sooty mold
Meloidogyne incognita (Kof. et White) Chitw.		root knot
Meloidogyne ovalis Riffle		ash root knot nematode
Microsphaera alni DC.		powdery mildew
Microstroma juglandis (Berang.) Sacc.		white mold
Morsus ulmi Holmes		elm phloem necrosis
Mycosphaerella caryigena Dem. et Cole		downy spot
Mycosphaerella cercidicola (Ell. et Kellerm.) Wolf		redbud anthracnose
Mycosphaerella dendroides (Cke.) Dem. et Cole		leaf blotch
Mycosphaerella effigurata (Schw.) House		ash leaf spot
Mycosphaerella fraxinicola (Schw.) House		ash leaf spot
Mycosphaerella glauca (Cke.) Woronichin		leaf spot and twig blight
Mycosphaerella juglandis Kessler		leaf spot
Mycosphaerella maculiformis (Pers.: Fr.) Schroet.		leaf spot

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Mycosphaerella milleri Hodges et Haasis	*Cercospora magnoliae* Ell. et Hark. (Imperfect state)	angular leaf spot
Mycosphaerella mori Wolf		leaf spot
Mycosphaerella nyssaecola (Cke.) Wolf		leaf spot
Mycosphaerella sassafras (Ell. et Ev.) Bub. et Kab.		sassafras leaf spot
Mycosphaerella taxi (Cooke) Lind		needle blight
Myxosporium nitidum Berk. et Curt.		twig blight
Naemacyclus minor Butin		needle cast
Nectria cinnabarina Tode: Fr.		branch dieback
Nectria coccinea Pers.: Fr. var. *faginata* Lohm., Wats. et Ay.		beech canker
Nectria galligena Bres.		Nectria canker
Nectria magnoliae Lohm. et Hept.		magnolia canker
Nectria peziza (Tode: Fr.) Fr.	*Nectria umbellulariae* (Plowr.) Harkn.	stem canker, dieback needle cast
Neofabraea populi G. E. Thompson		canker
Neopeckia coulteri (Pk.) Sacc.		pine brown-felt snow mold
Ovularia maclurae Ell. et Langl.		Osage-orange leaf spot
Oxyporus populinus (Sokum.: Fr.) Donk	*Fomes connatus* (Weinm.: Fr.) Gill.	heart rot
Paxillus involutus (Batch: Fr.) Fr.		brown root rot
Pellicularia koleroga Cke.	*Corticium stevensii* Burt.	thread blight
Peniophora polygonia (Fr.) Bourd. et Galz.	*Crytochaete polygonia* (Pers.) Karst.	trunk rot
Peniophora pseudo-pini Weres. et Gibs.		red heartwood stain
Peniophora rufa (Fr.) Boidin		trunk rot
Peniophora septentrionalis Laur.		trunk rot
Perenniporia compacta (Overh.) Ryv. et Gilbn.		white pocket rot
Perenniporia fraxinea (Bull.: Fr.) Ryv.	*Fomes fraxineus* (Bull.: Fr.) Cke.	wood rot
Perenniporia fraxinophilus (Peck) Ryv.	*Fomes fraxinophilus* (Pk.) Cke.	ash heart rot
Peridermium cerebroides Meinecke		coastal gall rust
Peridermium filamentosum Pk.		limb rust
Peridermium harknessii J. P. Moore	*Endocronartium harknessii* (J. P. Moore) Y. Hirat.	western gall rust
Peridermium ornamentale Arth.	*Pucciniastrum goeppertianum* (Kuehn) Kleb.	
Peridermium rugosum H. Jackson		needle rust
Peridermium stalactiforme Arth. et Kern		stalactiform rust
Pezicula acericola (Pk.) Sacc.		leaf spot
Pezicula subcarnea Groves		leaf spot or twig blight
Phacidium curtissii (Berk. et Rav.) Luttr.		leaf spot
Phacidium infestans Karst.		snow blight
Phaeocryptopus gaeumanni (Rohde) Petr.		needle cast
Phaeocryptopus nudis Petr.		needle cast
Phaeolus schweinitzii (Fr.) Pat.	*Polyporus schweinitzii* Fr.	red brown butt rot
Phellinus everhartii (Ell. et Gall) A. Ames	*Fomes everhartii* (Ell. et Gall.) Schr. & Spauld.	heart rot
Phellinus ferruginosus (Schrad.: Fr.) Pat.	*Poria ferruginosa* (Schrad.: Fr.) Karst.	white rot of slash
Phellinus igniarius (L.: Fr.) Quel.	*Fomes igniarius* (L.: Fr.) Kickx	false tender fungus
Phellinus johnsonianus (Murr.) Ryv.	*Fomes densus* Lloyd	heart rot
Phellinus laevigatus (Fr.) Bourd. et Galz.	*Fomes igniarius laevigatus* (Fr.) Overh.	heart rot
Phellinus nigrolimitatus (Rom.) Bourd. et Galz.	*Fomes nigrolimitatus* (Rom.) Egel.	root and butt rot
Phellinus pini (Thore: Fr.) A. Ames	*Fomes pini* (Thore: Fr.) Karst.	red ring rot
Phellinus pomaceus (Pers.) Maire	*Fomes pomaceus* (Pers.) Lloyd	trunk rot
Phellinus prunicola (Murr.) Gilbn.	*Poria prunicola* (Murr.) Sacc. et Trott.	trunk rot
Phellinus punctatus (Fr.) Pilat	*Poria punctata* (Fr.) Karst.	white rot of slash
Phellinus ribis (Schum.: Fr.) Quel.	*Fomes ribis* (Schum.: Fr.) Gill.	white heart rot

Scientific binomial	Synonym	Common name or symptom
Phellinus rimosus (Berk.) Pilat	*Fomes rimosus* (Berk.) Cke.	heart rot
Phellinus robustus (Karst.) Bourd. et Galz.	*Fomes robustus* Karst.	heart rot
Phellinus texanus (Murr.) A. Ames	*Fomes texanus* (Murr.) Hedgc. et Long	heart rot
Phellinus tremulae (Bond.) Bond. et Boriss	*Fomes igniarius* (L.: Fr.) Kickx var. *populinus* (Neum.) Campb.	false tinder fungus
Phellinus weiri (Murr.) Gilbn.	*Poria weirii* (Murr.) Murr.	laminated root rot
Phibalis pruinosa (Ell. et Ev.) Kohn et Korf		sooty-bark canker
Phleospora celtidis Ell. & Morg.		leaf spot
Phlyctaena tiliae Dearn.		leaf spot
Pholiota alnicola (Fr.) Singer	*Flammula alnicola* (Fr.) Kumm.	root and butt rot
Pholiota aurivella (Batsch: Fr.) Kumm.		
Pholiota destruens (Brond.) Gillet		heart rot
Pholiota hepatica (Huds.: Fr.) Singer	*Flammula alnicola* (Huds.: Fr.) Kumm.	beefsteak fungus
Pholiota limonella (Pk.) Sacc.	*Pholiota squarroso-adiposa* Lange	heart rot
Pholiota squarrosa (Muller: Fr.) Kumm.		root and butt rot
Phoma aposphaerioides Briard et Hariot		Phoma canker
Phoma harknessii Sacc.		bark saprophyte
Phoma hystrella Sacc.		yellow needle blight
Phoma pedunculi Ell. et Ev.		leaf spot
Phomopsis juniperovora Hahn		foliage blight
Phomopsis macrospora Kobayi & Chiba		Phomopsis canker
Phomopsis occulta Trav.		tip blight
Phoradendron bolleanum (Seem.) Eich. subsp. *densum* (Torr.) Fosb.		mistletoe
Phoradendron bolleanum (Seem.) Eich. subsp. *pauciflorum* (Torr.) Wiens		white fir mistletoe
Phoradendron flavescens (Pursh) Nutt.		eastern mistletoe
Phoradendron juniperinum Engelm. subsp. *juniperinum* Wiens		mistletoe
Phoradendron juniperinum Engelm. subsp. *libocedri* Wiens		incense-cedar mistletoe
Phoradendron longispicum Trel.		mistletoe
Phoradendron serotinum (Raf.) M. C. Johnst.		eastern leafy mistletoe
Phoradendron tomentosum (DC.) Gray		mistletoe
Phoradendron villosum (Nutt.) Nutt. subsp. *villosum* Wiens		western hairy mistletoe
Phyllachora perseae Hodges		redbay leaf spot
Phyllactinia corylea Pers.		powdery mildew
Phyllactinia guttata (Fr.) Lev.		powdery mildew
Phyllosticta celtidis Ell. et Kell.		leaf spot
Phyllosticta innumera Cke. et Harkn.		leaf spot
Phyllosticta maclurae Ell. et Ev.		leaf spot
Phyllosticta magnoliae Sacc.		magnolia leaf spot
Phyllosticta minima (Berk. et Curt.) Ell. et Ev.		tar spot
Phyllosticta opaca Ell. et Ev.		leaf spot
Phymatotrichum paulowniae Sacc.		leaf spot
Phymatotrichum omnivorum (Shear) Dugg.		Texas root rot
Physalospora gregaria Sacc.		twig blight
Physalospora ilicis (Schleich.: Fr.) Sacc.		leaf spot
Phytophthora cactorum (Leb. et Cohn) Schr.		damping-off
Phytophthora cinnamomi Rands		root rot
Phytophthora citricola Sevada		root rot
Phytophthora inflata Caros. et Tucker		elm canker
Phytophthora lateralis Tucker. et J. A. Milb.		root rot
Piggotia fraxini Berk. et Curt.		leaf spot
Piptoporus betulinus (Bull.: Fr.) Karst.	*Polyporus betulinus* Bull.: Fr.	heart rot
Pleurotus ostreatus (Jacq.: Fr.) Kumm.		oyster mushroom

Scientific binomial	Synonym	Common name or symptom
Pleurotus ulmarius (Bull.: Fr.) Kumm.		elm wood rot
Ploioderma hedgcokii (Dearn.) Darker	*Hypoderma hedgcokii* Dearn.	needle cast
Podosphaera oxyacanthae DC. var. *tridactyla* Wallr.		cherry powdery mildew
Pollaccia saliciperda (Allesch. et Tub.) v. Arx		willow blight
Polyporus abietinus Dicks.: Fr.	*Trichaptum abietinus* (Dicks.: Fr.) Ryv.	trunk rot
Polyporus adustus Willd.: Fr.	*Bjerkandera adusta* (Willd.: Fr.) Karst.	sapwood decay
Polyporus berkeleyi Fr.	*Bondarzewia berkeleyi* (Fr.) Bond et Singer	root rot
Polyporus caesius Schrad.: Fr.	*Postia caesia* (Schrad.: Fr.) Karst.	heart rot
Polyporus calkinsii (Murr.) Sacc. et Trott.		heart rot
Polyporus guttulatus Pk.		root rot
Polyporus hispidus Bull.: Fr.	*Inonotus hispidus* (Bull. ex Fr.) Karst.	hispidus canker
Polyporus lucidus Leys.: Fr.	*Ganoderma lucidum* (Leys. ex Fr.) Karst.	varnish or lacquer conk
Polyporus obtusus Berk.	*Spongipellis unicolor* (Schw.) Murr.	heart rot
Polyporus robiniophilus (Murr.) Lloyd	*Perenniporia robiniophila* (Murr.) Ryv.	heart rot
Polyporus squamosus Mich.: Fr.		scaly or saddleback fungus
Polyporus versicolor L.: Fr.	*Coriolus versicolor* (L.: Fr.) Quel.	sapwood decay
Poria albipellucida Baxt.	*Poria rivulosa* (Berk. et Curt.) Cke.	redwood ring rot
Poria asiatica (Pil.) Overh.		trunk rot
Poria ferruginosa (Schrad.: Fr.) Karst.	*Phellinus ferruginosus* (Schrad.: Fr.) Pat.	
Poria incrassata (Berk. et Curt.) Burt	*Serpula incrassata* (Berk. et Curt.) Donk	heart rot
Poria mutans (Pk.) Pk.		
Poria prunicola (Murr.) Sacc. et Trott.	*Phellinus prunicola* (Murr.) Gilbn.	trunk rot
Poria punctata (Fr.) Karst.	*Phellinus punctatus* (Fr.) Pilat	
Poria rimosa Murr.	*Diptomitoporus rimosus* (Murr.) Gilbn. et Ryv.	heart rot
Poria sequoiae Bonar		redwood trunk rot
Poria spiculosa Campb. et Davids.		canker rot of hickory and pecan
Poria subacida (Pk.) Sacc.	*Perenniporia subacida* (Pk.) Donk	white root conk
Pratylenchus penetrans Cobb		root lesion nematode
Pseudomonas lauracearum Harv.		leaf spot
Pseudomonas mori (Boy. et Lamb.) Stev.		bacterial leaf spot
Puccinia andropogonis Schw.		leaf rust
Puccinia cordiae Arth.		canker producing rust
Puccinia peridermiospora (Ell. et Tr.) Arth.		ash rust
Pucciniastrum epilobii Otth.		needle rust
Pucciniastrum goeppertianum (Keuhn) Kleb.	*Peridermium ornamentale* Arth.	needle rust
Pucciniastrum hydrangeae (Berk. et Curt.) Arth.		hemlock needle rust
Pucciniastrum vaccinii (Wint.) Jorst.		hemlock needle rust
Pyrofomes demidoffii (Lev.) Kotl. et Pouz.	*Fomes juniperinus* (Schrenk) Sacc. et Syd.	heart rot
Pythium debaryanum Hesse		damping-off
Pythium irregulare Buism.		damping-off and root rot
Pythium ultimum Trow.		damping-off
Pythium vexans de B.		root rot
Radulodon americanum Ryv.	*Radulodon caesearium* (Morg.) Ryvarden	trunk rot
Resinicium bicolor (Alb. & Schw.: Fr.) Parm.	*Odontia bicolor* (Alb. & Schw.) Bres.	white stringy rot
Retinocyclus abietis (Crouan) Graves et Wells		endophytic fungus
Rhabdocline pseudotsugae Syd.		needle cast
Rhizina undulata Fr.		root rot
Rhizoctonia crocorum (Pers.) DC. Fr.		root rot
Rhizoctonia solani Kuehn		damping-off
Rhizosphaera kalkoffii Bud.		needle cast
Rhytidiella baranyayi Funk et Zalasky		rough, corky bark
Rhytidiella moriformis Zalasky		rough bark
Rhytisma acerinum Pers.: Fr.		tar spot
Rhytisma punctatum Pers.: Fr.		tar spot
Rosellinia herpotrichioides Hept. et Davidson		grey mold
Russula delica Fr.		mycorrhizal symbiont
Russula xerampelina (Schaef.) Fr.		mycorrhizal symbiont

Scientific binomial	**Synonym**	**Common name or symptom**
Sarcotrichila alpina (Fuckel) Hoehn.		needle blight
Schizophyllum commune Fr.		sapwood rot
Schizoxylon microsporum Davidson et Lor.		Schizoxylon canker
Scirrhia acicola (Dearn.) Sigg.		brown spot
Scirrhia pini Funk et A. K. Parker		red band needle blight
Scleroderma hypogaeum Zeller		false puffball
Sclerotinia gracilipes (Cke.) Sacc.		sweetbay petal rot
Scytinostroma galactinum (Fr.) Donk	*Corticium galactinum* (Fr.) Burt	root and butt rot
Septobasidium burtii Lloyd		scale brown felt
Septobasidium pseudopedicellatum Burt		scale brown felt
Septogloeum celtidis Dearn.		leaf spot
Septoria aceris (Lib.) Berk. et Br.		leaf blister
Septoria angustissima Pk.		leaf spot
Septoria cornicola Desm.		dogwood leaf spot
Septoria musiva Pk.		septoria leaf spot
Septoria populicola Pk.		leaf spot and canker
Septoria quercicola (Desm.) Sacc.		oak leaf fungus
Septotinia podophyllina Wat.		leaf blotch
Serpula himantioides (Fr.) Karst.	*Merulius himantioides* Fr.	root and butt rot
Sirococcus clavigignenti-juglandacearum Nair, Kostichka, et Kuntz		butternut canker
Sirococcus strobilinus (Dearn.) Petr.		Sirococcus tip blight
Sphaerella umbellulariae Cke. et Harkn.		foliage discoloration
Sphaeropsis ulmicola Ell. et Ev.		elm canker
Sphaerotheca lanestris Harkn.		oak powdery mildew
Sphaerotheca phytophila Kellerm. et Swing.		powdery mildew
Sphaerulina taxi (Cke.) Mass.		yellow leaf scorch
Spongipellis delectans (Pk.) Murr.	*Polyporus delectans* Pk.	white rot of hardwoods
Spongipellis pachyodon (Pers.) Kotl. et Pouz.	*Irpex mollis* Berk. et Curt.	Irpex canker
Sporodesmium maclurae Thuem.		Osage-orange leaf spot
Steccherinum septentrionale (Fr.) Banker	*Hydnum septentrionale* Fr.	trunk rot
Stereum chailletii Pers.: Fr.	*Amylostereum chailletii* (Pers.: Fr.) Boid.	trunk rot
Stereum gausapatum (Fr.) Fr.		white heart rot
Stereum hirsutum (Willd.: Fr.) S. F. Gray		sapwood decay
Stereum murraii (Berk. et Curt.) Burt	*Cystostereum murraii* (Berk. et Curt.) Pouz.	trunk rot
Stereum sulcatum Burt	*Echinodontium sulcatum* (Burt) Gross	trunk rot
Strumella coryneoidea Sacc. et Wint.		Strumella canker
Suillus cothurnatus Sing.		mycorrhizal symbiont
Suillus granulatus (L.: Fr.) Kuntze	*Boletus granulatus* L.: Fr.	mycorrhizal symbiont
Suillus pictus (Pk.) Smith & Thiers	*Boletinus pictus* (Pk.) Smith & Thiers	mycorrhizal symbiont
Suillus subaureus (Pk.) Snell ex Slipp et Snell	*Boletus subaureus* (Pk.) Snell ex Slipp et Snell	mycorrhizal symbiont
Suillus subluteus (Pk.) Snell ex Slipp et Snell	*Boletus subluteus* Pk.	mycorrhizal symbiont
Taphrina caerulescens (Mont. et Desm.) Tul.		oak leaf blister
Taphrina carveri Jenk.		tar spot
Taphrina cerasi (Fckl.) Sadeb.		cherry leaf curl
Taphrina johansonii Sadeb.		catkin deformity
Taphrina populi-salicis Mix		yellow leaf blister
Thyronectria austro-americana (Speg.) Seeler		honeylocust wilt
Trametes serialis Fr.	*Coriolellus serialis* (Fr.) Murr.	heart rot
Tranzschelia pruni-spinosae (Pers.) Diet.		cherry rust
Tricholoma flavovirens (Pers.: Fr.) Lund.		mycorrhizal symbiont
Tuber griseum Pers.: Fr.	*Tuber magnatum* Pico in Vitt.	mycorrhizal symbiont
Tuber melanosporum Vitt.		mycorrhizal symbiont
Tylopilus felleus (Bull.: Fr.) Karst.	*Boletus felleus* Bull.: Fr.	mycorrhizal symbiont
Tympanis pinastri (Pers.: Fr.) Tul.		bark saprophyte
Tyromyces amarus (Hedgc.) Lowe	*Polyporus amarus* Hedgc.	pocket dry rot

Checklist of Organisms Causing Tree Diseases

Scientific binomial	Synonym	Common name or symptom
Tyromyces balsameus (Pk.) Murr.	*Polyporus balsameus* Pk. (See also *Climacocystis*)	brown cubical rot
Tyromyces borealis (Fr.) Imaz.	*Polyporus borealis* Fr.	heart rot
Tyromyces spraguei (Berk. et Curt.) Murr.	*Polyporus spraguei* Berk. et Curt.	root rot
Uncinula circinata Cke. et Pk.		powdery mildew
Uncinula clintonii Pk.		powdery mildew
Uncinula flexuosa Pk.		powdery mildew
Uncinula salicis Wint.		powdery mildew
Uredinopsis pteridis Diet. et Holw. in Diet.	*Uredinopsis macrosperma* Cke.	needle rust
Uredinopsis struthiopteridis Stormer		needle rust
Uromyces digitatus Wint.		koa leaf blister
Uromyces koae Arth.		koa witches' broom
Ustulina vulgaris Tul.		wood rot
Ustulina deusta (Hoff.: Fr.) Lind.		trunk rot
Valsa kunzei Fr.		canker
Venturia acerina Plak.		leaf spot
Venturia macularis (Fr.) Mull. et v. Arx	*Venturia tremulae* Aderh.	shepherd's crook shoot blight
Venturia populina (Vuill.) Fabrici		shepherd's crook shoot blight
Verticicladiella wageneri Kend.	*Ceratocystis wageneri* Goheen et Cobb (Perfect state)	black stain root rot
Verticillium albo-atrum Reinke et Berth.		Verticillium wilt
Virgella robusta (Tub.) Darker		needle cast
Virus - Cucumber mosaic		cucumber mosaic virus
Virus - Maclura mosaic		Maclura mosaic virus
Virus - *Morsus ulmi*		elm phloem necrosis virus
Wolfiporia cocos (Wolf) Ryv. et Gilbn.	*Poria cocos* Wolf	brown root and butt rot
Xiphinema americanum Cobb		dagger nematode
Xylobolus frustulatus (Pers.: Fr.) Boidin		white pocket rots of hardwoods

Checklist of Birds

Common name	Scientific name[1]
Bananaquit	*Coereba flaveola*
Bluebird, Mountain	*Sialia currucoides*
Bobwhite, Northern	*Colinus virginianus*
Cardinal	*Cardinalis cardinalis*
Chachalaca, Plain	*Ortalis vetula*
Chickadee, Black-capped	*Parus atricapillus*
Crossbill,	
Red	*Lorix curvirostra*
White-winged	*Lorix leucoptra*
Crow	*Corvus spp*
Fish	*Corvus ossifragus*
Dove, Mourning	*Zenaida macroura*
Duck, Wood	*Aix sponsa*
Eagle,	
Bald	*Haliaeetus leucocephalus*
Golden	*Aquila chrysaetos*
Egret, Great	*Casmerodius albus*
Finch, Purple	*Carpodacus purpureus*
Flicker, Northern	*Colaptes auratus*
Goldeneye, Common	*Bucephala clangula*
Goldfinch, American	*Carduelis tristis*
Grackle, Common	*Quiscalus quiscula*
Grosbeak,	
Evening	*Coccothraustes vespertinus*
Pine	*Pinicola enucleator*
Rose-breasted	*Pheucticus ludovicianus*
Grouse,	
Blue	*Dendragapus obscurus*
Spruce or Franklin's	*Dendragapus canadensis*
Ruffed	*Bonasa umbellus*
Sharp-tailed	*Tympanuchus phasianellus*
Gull, Ring-billed	*Larus delawarensis*
Hawk, Red-tailed	*Buteo jamaicensis*
Jay,	
Blue	*Cyanocitta cristata*
Pinyon	*Gymnorhinus cycanocephalus*
Scrub	*Aphelocoma coerulescens*
Steller's	*Cyanocitta stelleri*
Junco, Dark-eyed	*Junco hyemalis*
Kinglet,	
Golden-crowned	*Regulus satrapa*
Ruby-crowned	*Regulus calendula*
Mallard	*Anas platyrhynchos*
Mockingbird, Northern	*Mimus polyglottus*
Nutcracker, Clark's	*Nucifraga columbiana*
Nuthatch,	
Brown-headed	*Sitta pusilla*
Red-breasted	*Sitta canadensis*
White-breasted	*Sitta carolinensis*
Osprey, American	*Pandion haliaetus*
Ovenbird	*Seiurus aurocapillus*
Owl, Great Gray	*Strix nebulos*
Parakeet, Carolina	extinct
Parrot, Puerto Rican	*Amazona vittata*
Partridge, Hungarian	*Perdix perdix*
Parula, Northern	*Parula americana*
Pheasant, Ring-necked	*Phasianus colchicus*
Pigeon	*Columba spp*
Band-tailed	*Columba gasciata*
Prairie-chicken, Greater	*Tympanuchus cupido*
Quail, California	*Callipepla californica*
Redpoll, Common	*Carduelis flammea*
Reina Mora	*Spindalis zena*
Robin, American	*Turdus migratorius*
Sapsucker,	
Red-breasted	*Sphyrapicus ruber*
Williamson's	*Sphyrapicus thyroideus*
Yellow-bellied	*Sphyrapicus varius*
Siskin, Pine	*Carduelis pinus*
Sparrow,	
Black-throated	*Amphispiza bilineata*
Song	*Melospiza melodia*
White-throated	*Zonotrichia albicollis*
Starling, European	*Sturnus vulgaris*
Tanager, Striped-headed	*Spindalis zena*
Thrasher, Pearly-eyed	*Margarops suscatus*
Thrush,	
Red-legged	*Turdus blumbea*
Varied	*Ixoreus narvius*
Turkey, Wild	*Meleagris gallopavo*
Veery	*Cathatus fuscescens*
Warbler,	
Bachman's	*Vermivora bachmanii*
Black-and-white	*Mniotilta varia*
Blackburnian	*Dendroica fusca*
Black-throated Green	*Dendroica virens*
Cape May	*Dendroica tigrina*
Kirtland's	*Dendroica kirtlandii*
Magnolia	*Dendroica magnolia*
Nashville	*Vermivora ruficapilla*
Pine	*Dendroica pinus*
Prothonotary	*Protonotaria citrea*
Yellow-throated	*Dendroica dominica*
Waxwing,	*Bombycilla spp*
Bohemian	*Bombycilla garrulus*
Cedar	*Bombycilla cedrorum*
Woodcock, American	*Scolopax minor*
Woodpecker,	
Acorn	*Melanerpes formicivorus*
Downy	*Picoides pubescens*
Hairy	*Picoides villosus*
Pileated	*Dryocopus pileatus*
Red-bellied	*Melanerpes carolinus*
Red-cockaded	*Picoides borealis*
Red-headed	*Melanerpes erythrocephalus*
White-headed	*Picoides albolarvatus*
Yellowthroat, Common	*Geothlypis trichas*

Checklist of Mammals

Common name	Scientific name
Agouti	*Dasyprocta* or *Myoprocta* spp.
Bat, Jamaican Fruit-eating	*Artibus jamaicensis*
Bear,	
Black	*Ursus americanus*
Grizzly	*Ursus arctos*
Beaver,	
American	*Castor canadensis*
Mountain	*Aplodontia rufa*
Bighorn Sheep	*Ovis canadensis*
Bison	*Bison bison*
Caribou (Woodland)	*Rangifer tarandus*
Chickaree (Red Squirrel)	*Tamiasciurus* spp.
Chipmunk	*Tamias* spp.
Cliff	*Tamias dorsalis*
Eastern	*Tamias striatus*
Least or Western	*Tamias minimus*
Cottontail (American Rabbit)	*Sylvilagus* spp.
Desert	*Sylvilagus audubonii*
Eastern	*Sylvilagus floridanus*
Mountain	*Sylvilagus nuttallii*
New England	*Sylvilagus transitionalis*
Coyote	*Canis latrans*
Deer,	
Black-tailed or Mule	*Odocoileus hemionus*
White-tailed	*Odocoileus virginianus*
Elk (Wapiti)	*Cervus elaphus*
Roosevelt	*Cervus elaphus roosevelt*
Fox,	
Gray	*Urocyon cinereoargenteus*
Red	*Vulpes vulpes*
Ground Squirrel,	
Golden-mantled	*Spermophilus lateralis*
Thirteen-lined	*Spermophilus tridecemlineatus*
California or Beechey's	*Spermophilus beecheyi*
Hare	*Lepus* spp.
Snowshoe	*Lepus americanus*
Jack Rabbit	*Lepus* spp.
Lynx, Canadian	*Lynx canadensis*
Marmot, Hoary	*Marmota caligata*
Marten, Pine	*Martes americana*
Mice, Meadow (Voles)	*Microtus* spp.
Moose	*Alces alces*
Mountain Goat	*Oreamnos americanus*
Mouse,	
California	*Peromyscus californicus*
Deer	*Peromyscus maniculatus*
Pinyon	*Peromyscus truei*
White-footed	*Peromyscus leucopus*
Nutria	*Myocastor coypus*
Opossum, Virginia	*Didelphis virginiana*
Peccary	*Tayassu* spp.
Pika	*Ochotona princeps*
Pocket Gopher,	
Eastern	*Geomys* spp.
Western	*Thomomys* spp.
Porcupine	*Erethizon dorsatum*
Rabbit (American)	*Sylvilagus* spp.
Brush	*Sylvilagus bachmani*
Swamp	*Sylvilagus aquaticus*
Raccoon	*Procyon lotor*
Rat (Old World)	*Rattus* spp.
Polynesian	*Rattus exulans*
Tree	*Rattus rattus*
Shrew (Red-toothed)	*Sorex* spp.
Skunk	*Conepatus* spp.
Squirrel (Flying)	*Glaucomys* spp.
Squirrel (Red)	*Tamiasciurus* spp.
Douglas'	*Tamiasciurus douglasii*
Pine, Red, or Spruce	*Tamiasciurus hudsonicus*
Squirrel (Tree)	*Sciurus* spp.
Abert's (Kaibab)	*Sciurus aberti*
Eastern Fox	*Sciurus niger*
Eastern Gray	*Sciurus carolinensis*
Western Gray	*Sciurus griseus*
Vole (Meadow)	*Microtus* spp.
Creeping or Oregon	*Microtus oregoni*
Montane	*Microtus montanus*
Vole (Pine)	*Pitymys* spp.
Pine or Woodland	*Pitymys pinetorum*
Vole (Red-backed)	*Clethrionomys* spp.
Gapper's Red-backed	*Clethrionomys gapperi*
Wild Pig	*Sus scrofa*
Wolf, Gray or Timber	*Canis lupus*
Wolverine	*Gulo gulo*
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